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FOREWORD

The Commonwealth Scientific and Industrial Research Organization, in collaboration with the Australian National Research Council, has decided to publish this new periodical, the Australian Journal of Zoology, as a medium for the publication of results of original scientific research in zoology with special emphasis on descriptive aspects.

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THE ECOLOGY OF *CHRYSOMELA GEMELLATA* ROSSI AND *C. HYPERICI* FORST., AND THEIR EFFECT ON ST. JOHN'S WORT IN THE BRIGHT DISTRICT, VICTORIA

By L. R. CLARK*

[*Manuscript received March* 13, 1952]

Summary

This paper describes the basic entomological study necessary in an investigation of the effectiveness of *Chrysomela gemellata* Rossi and *C. hyperici* Forst. as controls of St. John's wort, *Hypericum perforatum* L. var. *angustifolium* DC, in the Bright district, Victoria.

The investigation has shown that the conditions prevailing in the Bright district during the study period must have been generally near the limit of tolerance of both *C. gemellata* and *C. hyperici,* parts being a little above and parts definitely below this limit. Furthermore, largely because of certain behaviour responses, neither insect has been able to colonize the timbered areas infested by *Hypericum.* The total area favouring the multiplication of the insects forms only a small part of the area colonized successfully by *Hypericum.*

Within the zone favourable to the beetles, they have failed to control *Hypericum* effectively except in small, treeless areas adjoining densely timbered country infested by the weed (in such places the timbered area has acted as a damping factor to population fluctuation, enabling the insects to persist in moderate numbers). Although adverse conditions have played an important part in limiting the effectiveness of the insects, their failure has been due primarily to their own characteristics. Both species have poor powers of dispersal and a relatively poor ability to multiply.

In the most favourable sites, both species are able to multiply within a few years to a density high enough to cause complete defoliation of the host plant, which usually dies out. By destroying their food and reducing their protective cover, both species suffer very heavy losses and greatly limit their own numbers. Although many individuals succumb to starvation, a large proportion of the mortality is caused by density-independent factors, e.g. frost and predation, which are allowed to operate in an intensified manner by removal of the protective cover provided by the foliage of the host plant.

After completing the defoliation of the weed, the surviving beetles migrate elsewhere in search of more food. Their desertion of the site gives the host plant a chance to recover by regeneration from seed. Numerous environmental factors unfavourable to the insects, combined with their poor mobility and slow rate of increase, frequently allow the plant to recover almost completely before beetle numbers become sufficiently high to defoliate it again.

Where other wort-controlling agencies are lacking, the insects have caused their host plant to fluctuate violently in density in both space and time without producing a great overall reduction in quantity. By destroying stands of *Hypericum* in areas in which the soils are capable of growing a dense pasture, the insects have paved the way for successful wort control by other factors, e.g. shade-producing herbage and grazing animals. Such areas virtually cease to provide habitats for the insects after the original stand of *Hypericum* is destroyed.

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Table 1

MEASUREMENTS OF EGG WIDTH FOR 15 SAMPLES OF 50 EGGS OF *C. HYPERICI*

Sample No.	Frequency Distributions										Sample Mean and Standard Error	Notes
	Mid-points of Classes (micrometer units)									Total		
	7.375	7.875	8.375	8.875	9.375	9.875	10.375	10.875	11.375			
1				6	4	32	6	2		50	9.86 ± 0.06	Eggs less than 3 days old from oviposition cages
2				9	10	25	5	0	1	50	9.73 ± 0.11	
3				3	14	25	5	2	1	50	9.84 ± 0.07	
4		2	1	9	12	18	7	1		50	9.61 ± 0.08	
5			2	18	13	14	3			50	9.40 ± 0.07	
6		3	2	16	15	11	3			50	9.32 ± 0.08	
7				7	9	23	10	1		50	9.82 ± 0.07	Eggs just about to hatch from oviposition cages
8				4	11	27	5	3		50	9.83 ± 0.07	Eggs at all stages of development from the field, those in which development was about half complete predominating
9	1	0	0	5	6	29	8	1		50	9.80 ± 0.05	
10					10	31	7	2		50	9.91 ± 0.05	
11				9	15	20	6			50	9.65 ± 0.07	
12				13	13	19	5			50	9.60 ± 0.06	
13				7	19	20	4			50	9.62 ± 0.05	
14			2	12	10	23	3			50	9.55 ± 0.07	
15				18	11	15	5	1		50	9.53 ± 0.08	
Total	1	5	7	136	172	332	82	13	2	750		

Mean for all eggs = 9.67 micrometer units = 0.460 mm. approx.

Estimate of the probability of occurrence of eggs equal to or less than 10 micrometer units in width = 653/750 = 0.871.

I. INTRODUCTION

The closely related beetles, *Chrysomela gemellata* Rossi and *C. hyperici* Forst., were introduced to Australia some years ago in an attempt to control St. John's wort, *Hypericum perforatum* L. var. *angustifolium* DC (Wilson 1943). Both insects were first liberated in the Ovens Valley near Bright, Victoria, where they have destroyed dense infestations of the weed in recent years.

The progress shown by the insects led the author to undertake an investigation to ascertain the parts played by various factors in determining their effectiveness as controls of the weed. An essential part of the investigation was a detailed study of the ecology of each insect in the Bright district. This was not possible until methods were developed for the identification of the immature stages of the insects, which usually occurred in mixed populations.

This paper describes the entomological aspects of the investigation, which began early in 1948 and ended in 1951.

II. IDENTIFICATION OF THE SPECIES

In his study of the insect fauna of *Hypericum*, Wilson (1943) described a method for identifying the adults of *C. gemellata* and *C. hyperici*. As similar information was not available for the immature stages, procedures for distinguishing them had to be devised before starting the ecological study. The writer has obtained no evidence to suggest that these insects ever interbreed, and consequently has assumed that two distinct populations were involved.

Each year *C. gemellata* emerged from aestivation and began ovipositing approximately 6 weeks before *C. hyperici* (Section IV). This enabled not only the collection of mature adults of the species, but also the collection of all four larval stages before any eggs of *C. hyperici* had hatched. Similarly the pupae of *C. gemellata* could be obtained long before those of *C. hyperici* appeared. Mature adults of *C. hyperici*, together with eggs, larvae, and pupae, were obtained from three areas uncolonized by *C. gemellata*.

(*a*) *Egg Stage*

Approximately 600 adults of each species were collected from the field in 1948, 1949, and 1950, and placed out of doors in wire-gauze cages in which temperature and humidity conditions resembled those occurring naturally. The insects were supplied daily with fresh shoots of *Hypericum* on which they fed and oviposited. Eggs were obtained as required by making random collections from the shoots. The eggs of each species were attached singly, or in small batches, to the leaves of the weed by a small quantity of dried secretion, and were easily removed.

Preliminary examinations of the eggs of each species showed that the small differences in coloration were not sufficiently consistent to permit reliable separation. Differences in size offered the only possible means of rapid separation.

(i) *Separation by Size Differences*.—Frequency distributions for measurements of egg length and maximum width (hereafter referred to as width)

TABLE 2

MEASUREMENTS OF EGG WIDTH FOR 15 SAMPLES OF 50 EGGS OF *C. GEMELLATA*
(ALL TAKEN FROM BREEDING CAGES)

Sample No.	Frequency Distributions									Total	Sample Mean and Standard Error	Notes
	Mid-points of Classes (micrometer units)											
	8.875	9.375	9.875	10.375	10.875	11.375	11.875	12.375	12.875			
1			13	11	22	3	1			50	10.63 ± 0.11	Eggs less than 3 days old
2			8	11	19	7	5			50	10.84 ± 0.08	Eggs less than 3 days old
3			14	11	24	0	1			50	10.58 ± 0.04	Eggs less than 3 days old
4	1	2	7	15	19	6				50	10.54 ± 0.08	Eggs less than 3 days old
5	1	1	10	12	22	4				50	10.55 ± 0.08	Development approximately half complete
6			4	11	27	8				50	10.82 ± 0.06	Almost fully developed
7			5	11	24	7	2	0	1	50	10.86 ± 0.09	Almost fully developed
8			2	4	22	18	3	1		50	11.01 ± 0.07	Development approximately half complete
9			5	4	32	5	4			50	10.90 ± 0.07	Development approximately half complete
10	2	4	9	17	16	2				50	10.40 ± 0.08	Various stages of development
11	1	2	14	21	11	0	1			50	10.36 ± 0.07	Various stages of development
12	1	0	12	21	15	1				50	10.46 ± 0.06	Various stages of development
13			15	14	19	1	1			50	10.52 ± 0.08	Various stages of development
14		3	15	15	13	2	2			50	10.45 ± 0.08	Almost fully developed
15		1	14	20	15					50	10.44 ± 0.06	Almost fully developed
Total	6	13	147	198	300	64	20	1	1	750		

Mean for all eggs = 10.62 micrometer units = 0.506 mm. approx.
Estimate of the probability of the occurrence of eggs equal to or less than 10 micrometer units in width = 166/750 = 0.221.

showed a considerable overlap in the ranges for each dimension, that for length being the greater. In a random sample of 100 day-old eggs of each species, it was found that 84 of the *C. hyperici* eggs were equal to or less than 10 micrometer units in width (0.476 mm.), whereas only 18 *C. gemellata* eggs had widths equal to or less than this value. As 10 micrometer units was a very convenient limit for dividing the eggs of each species into two groups, its value as a means of separating the eggs in mixed field samples was examined.

After ascertaining that the eggs of each species did not change appreciably in surface area during development, measurements (Tables 1 and 2) were made of the widths of eggs at various stages of development laid between mid May and late July, i.e. over the period when eggs of both species are fairly plentiful. The frequency distributions for *C. hyperici* (Table 1) show that few eggs exceeded 10 units in width, the mean percentage being approximately 13. The estimated probability that an egg of *C. hyperici* would be equal to or less than 10 units in width was 0.871. The corresponding probability for *C. gemellata* was 0.221 (Table 2). The sample means for *C. gemellata* were all significantly higher than those for *C. hyperici*. The frequency distributions for the pooled samples were very similar in form, the curve for each species exhibiting negative skewness and a slight "hump" to the left of the mode.

The method tested for the separation of eggs in mixed field samples may be described as follows: Let a be the probability that an egg of *C. hyperici* will be equal to or less than 10 micrometer units in width, and b be the similar probability for an egg of *C. gemellata*. Let x be the number of *C. hyperici* eggs in a mixed sample of N eggs. Then $N-x$ is the number of *C. gemellata* eggs. Let z be the total number of eggs in the sample equal to or less than 10 units in width. Then if the sample is large and eggs of both species are numerous, z would nearly equal $ax+b(N-x)$. Consequently x would differ very little from $(z-bN)/(a-b)$, and an approximate estimate of the number of *C. hyperici* eggs ($\hat{x}$) is given by the formula $\hat{x}=(z-bN)/(a-b)$. The estimates of a and b obtained by sampling were 0.871 and 0.221 respectively. These estimates were used in the formula $\hat{x}=(z-0.221N)/(0.871-0.221)$. If x is estimated in this way its fiducial distribution has an approximate variance of

$$\frac{\sigma a_1{}^2(z-0.221N)^2+\sigma b_1{}^2(z-0.871N)^2}{(0.871-0.221)^4}$$

where a_1 and b_1 are the unknown actual proportions of *C. hyperici* and *C. gemellata* eggs in the sample either equal to or less than 10 units in width, and $\sigma a_1{}^2$ and $\sigma b_1{}^2$ are the variances of their estimates, which can be determined approximately (Appendix I).

The method was tested on mixed samples of known numbers of *C. gemellata* and *C. hyperici* eggs. When 50 eggs of each species were used the 0.05 fiducial limits of the estimates were in the vicinity of ± 25, showing that the method was not precise. The standard error of the estimate for a particular species was found to decrease as the proportion of that species increased and vice versa. In spite of its defects, the method had to be used in replicated population studies carried out in 1949. Fortunately, a large proportion of the *C. gemellata* eggs were laid before oviposition by *C. hyperici* began and were therefore identified without error.

(ii) *Separation by Number of Pairs of Larval "Egg-bursters".*—As described below, the first-instar larva of *C. hyperici* has only three pairs of functional egg-bursting spines whereas five pairs are present in *C. gemellata.* These structures became heavily pigmented shortly before eclosion and could be seen readily through the chorion. Thus if eggs were kept until they had hatched or were just about to hatch they could be identified accurately. The exceptions, of course, were infertile eggs, which appeared to be produced in slightly higher numbers by *C. gemellata* than by *C. hyperici.* The percentage infertility in mixed samples was generally of the order of 1-10 per cent. (Section VIII).

After the limitations of the measurement method were appreciated, the eggs collected in population samples were allowed to complete development in the laboratory. The small numbers of infertile eggs were divided arbitrarily between the species in the proportions in which fertile eggs occurred. The error involved was of no practical importance.

(*b*) *Larval Stage*

(i) *First-Instar Larva.*—The examination of 150 first-instar larvae of *C. hyperici*, hatching from eggs laid in outdoor cages, showed that none possessed more than three pairs of egg-bursting spines. These heavily chitinized processes were situated on the mesonotum, metanotum, and first abdominal notum. A few individuals had, in addition, a pair of minute dark spots on the second abdominal notum or on both the second and third. These tiny structures appeared to be vestigial egg-bursters. A similar examination of *C. gemellata* larvae showed that 148 out of 150 possessed five pairs of apparently functional egg-bursters. Two larvae had a single spine missing. In all specimens the egg-bursters on the second and third abdominal nota were much larger than the corresponding minute structures present on a few *C. hyperici* larvae. Thus the difference in the number of pairs of egg-bursters appeared to be a satisfactory criterion for the separation of the species.

(ii) *Older Larvae.*—It was necessary to depend on size differences for the separation of the second-, third-, and fourth-instar larvae. Fortunately, the author was concerned principally with the separation of larval populations living in the presence of an adequate food supply. The obvious dimension to test was the maximum width of the head capsule. This was taken as the distance between the two projecting ocelli, which appear at the widest section of the head when the larva is held on its back.

The results of the measurements are summarized in Table 3, in which data for the first instar are included as a matter of interest. The material for each instar was composed of 25 larvae reared at the Field Station and 50 individuals collected in the field. The size ranges for the reared larvae and those collected in the field were similar in all cases. The differences between the means given in Table 3 are, of course, highly significant. The ratios of the means for successive instars and their means indicate that head width follows a regular geometrical progression in the successive instars of both species (i.e. Dyar's Law, 1890; see Imms 1934) with the same common ratio.

TABLE 3

WIDTH OF HEAD CAPSULE IN LARVAE OF *C. GEMELLATA* AND *C. HYPERICI*
(75 individuals of each instar)

Instar	Mean Head Width and Standard Error (micrometer units)	Range (micrometer units)	Approximate Mean Head Width (mm.)	Approximate Range (mm.)
First				
C. gemellata	10.49 ± 0.06	9.25-11.50	0.50	0.44-0.55
C. hyperici	9.22 ± 0.10	8.00-10.25	0.44	0..38-0.49
Second				
C. gemellata	15.23 ± 0.05	14.00-16.50	0.72	0.67-0.79
C. hyperici	13.09 ± 0.05	12.00-14.50	0.62	0.57-0.69
Third				
C. gemellata	22.05 ± 0.09	20.00-24.00	1.05	0.95-1.14
C. hyperici	18.58 ± 0.09	17.00-20.00	0.88	0.81-0.95
Fourth				
C. gemellata	30.31 ± 0.10	28.00-33.00	1.44	1.33-1.57
C. hyperici	26.43 ± 0.11	24.00-28.50	1.26	1.14-1.36

Ratios of means for successive instars:

	Second/First	Third/Second	Fourth/Third	Mean Ratio
C. hyperici	1.42	1.42	1.42	1.42
C. gemellata	1.45	1.45	1.37	1.42

Arbitrary size limits selected for the different instars (micrometer units):

	Second	Third	Fourth
C. hyperici	up to 14.0	> 16.5 - 20.0	> 24.0 - 28.5
C. gemellata	> 14.0 - 16.5	> 20.0 - 24.0	> 28.5

The ranges show a small overlap between corresponding instars and between the third instar of *C. gemellata* and the fourth instar of *C. hyperici*. When the data were arranged in a frequency distribution it was found that very few individuals were involved in the overlaps. By using the arbitrary size limits given in Table 3 for separation of the larval stages very few wrong identifications were made. It was therefore decided to use them for the separation of the material collected in population sampling. In this work, large numbers and numerous samples were usually involved and highly accurate identification was not essential. However, as the majority of *C. gemellata* larvae passed through each stage before any *C. hyperici* reached it, identification with almost 100 per cent. accuracy was frequently possible. As a standard procedure, "border-line" individuals of doubtful identity were allotted automatically to the species most numerous at the time in the instar concerned.

(c) *Pupal Stage*

As no suitable taxonomic criteria were found for this stage, the pupae in population samples were brought in from the study areas and allowed to complete development to the adult stage in the laboratory. Great care had to be exercised in handling this stage. It was necessary to remove the pupae of each species from their cells in the soil by means of a soft camel-hair brush or a grass leaf. They were placed in small glass tubes padded with cotton wool and carried to the laboratory, where they were kept in a large container at a relative humidity of approximately 100 per cent. In this way it was possible to obtain survivals of 90 per cent. or higher. The few individuals that died were divided between the species in the proportions in which survivors occurred.

III. General Description of Procedures used in the Ecological Study

A large part of the study was carried out in the field. Supplementary observations and experiments were made either in three plots of *Hypericum* situated in the grounds of the Field Station at Bright or in the laboratory. Details of the numerous methods used are given with the results obtained in the sections which follow. At this stage, however, a general outline of procedures is necessary.

(a) *The Study Areas*

Three principal classes of habitat in which *Hypericum* is the predominant herbaceous species may be recognized in the Bright district. In each the plant exhibits a somewhat different growth form. These classes are not altogether mutually exclusive, but may be considered so for present purposes. They are:

(i) Areas cleared of timber in which fairly deep soils are present. The majority were once used for cereal cropping. They are now occupied by very dense stands of the weed. The individual crowns (see Clark and Clark 1952) produce a tall, dense growth of flowering stems in the spring, and large, dense interlacing "mats" of procumbent stems during the autumn and winter (Plate 1). Such areas were termed "dense wort" habitats.

(ii) Areas cleared of timber in which the soils are shallow or stony. In many instances the soil has been reduced to a rubble of sand and stones by gold dredging. *Hypericum,* although a dominant species, and on stony gold dredgings sometimes the only plant, is normally much smaller than in (i) and sparser in growth habit. The crown density may exceed that in (i), but the quantity of *Hypericum* foliage per unit area is always much less (Plate 2). Such areas were termed "sparse wort" habitats.

(iii) Eucalypt forest (trees about 40 years old) or pine plantations (trees about 10 years old) in which the stand of *Hypericum* is sometimes of higher crown density than in (i), but always composed of relatively small individuals characterized by a single, slender flowering stem and a relatively open "mat"

(Plate 3). Such areas were termed "timbered" habitats. As far as *C. gemellata* and *C. hyperici* were concerned, the principal differences between these areas and (i) and (ii) were reduced solar and ground radiation, and far more litter at the soil surface, due, of course, to the presence of dense timber. The total area of *Hypericum*-infested forests and plantations greatly exceeded the total treeless area infested by the weed.

The study of population changes in *C. gemellata* and *C. hyperici* was carried out in study areas representative of these three classes of habitat. As both species exhibited marked aggregation in the field, it was necessary to use very small areas for population sampling (0.4-1.0 sq. ch.). Only in such areas was it possible to obtain distributions fairly close to random. The magnitude of the numbers present also had to be used as a criterion for the selection of study areas. For a valid comparison of the favourableness of different types of habitat it was essential to have sites in which *Chrysomela* numbers would remain too low to cause marked defoliation of the host plant, i.e. too low to cause significant reduction of the local supply of food and cover. On the other hand, numbers had to be as high as possible for statistical analysis. Thus plot selection was a matter of careful judgment; and, to ensure some replication in the final results, the author was forced to begin with a large number of areas. Population numbers in most study areas were found to be suitable for intensive sampling only for one season.

The study areas were divided into four to ten equal sampling sectors, depending on the size. At intervals ranging from 1 to 5 weeks, estimations of population density were made by taking one or two random samples (either 2 by 2 or 3 by 3 lk.) from the central part of each sector. All *Chrysomela* stages present in the sample quadrats were collected and taken to the laboratory, where they were identified and counted. When estimates of the amount of plant cover associated with *Chrysomela* numbers were required, the herbaceous material in the sample quadrats was collected, separated into *Hypericum*, other species, and debris, and air-dried to approximately constant weight. This enabled the computation of mean values for each major component of the cover present during a particular period.

For the study of survival for the period from oviposition to adult emergence from pupation, study areas were selected throughout the small Bright district, treeless areas being located close to timbered areas so that paired comparisons could be made. In addition to being numbered, these areas are labelled "*a*", "*b*", and "*c*" to denote dense wort, sparse wort, and timbered habitats, respectively, in later sections of the paper. There was no difficulty in finding areas of all three types containing suitable populations of *C. hyperici*. However, only one area of eucalypt forest was found in which numbers of *C. gemellata* were sufficiently high. In 1950, attempts were made to produce suitable numbers of this species in forest sites, including that used in 1949, by liberating reproducing adults; but all except one failed as the insects disappeared within two or three days. They laid an adequate number of eggs only in the forest site used in 1949.

For the period from oviposition to adult emergence, the survival rate of each species was computed as a/b where a was the estimated total number of adult beetles produced per unit area and b the estimated total egg production per unit area. The variance of each survival rate was computed as

$$\frac{a^2.\ \text{variance}\ b + b^2.\ \ \text{variance}\ a}{b^4}.$$

The variances of the adult numbers were determined in the usual way. The special methods necessary for estimating the variances of the egg numbers are described later (Section VI and Appendix II). For each study area the ratio

$$\frac{x - y}{\sqrt{\text{Variance}\ x + \text{variance}\ y}}$$

was used to determine the significance of the difference between the survival rate of each species (x and y). This ratio must have a value of at least 2.6 for a difference to be significant at the 1 per cent. level. This was taken as the minimum for significant differences in individual comparisons because the variances associated with the estimates of survival rates and total eggs were approximations.

Different study areas of similar size were used for the investigation of subsequent numerical changes in the adult populations of each species. Throughout the paper they are indicated by numbers only. New areas were used firstly because adult numbers became too low in some of the other areas for further counts; and secondly because the latter areas would have been damaged considerably by further sampling. The estimation of population changes was limited to:

(i) The period immediately before aestivation, and

(ii) the aestivation period.

Population changes were estimated in terms of the differences between the population densities of each insect at the beginning and end of the interval concerned. The associated variances were determined by the usual simple methods.

The mortality occurring during the period from adult emergence until aestivation could not be assessed reliably owing to variable migration, which commenced a few weeks after the adults appeared. The rough estimates possible suggest that the overall survival rate for this interval was of the order of 50-75 per cent. for both species.

(*b*) *The Type Sites*

It was necessary for the population studies on the chrysomelids to obtain approximate estimates of the times spent in the egg and larval stages at different times of the year. Various difficulties made it impossible to carry out the required detailed observations in the study areas. Consequently, three "type sites" were set up at the Field Station on suitable soils by transplanting mature

Hypericum in large blocks of earth containing most of the root system of each crown and bearing the natural accumulation of debris on the surface. Plots of living weed were produced in which plant form, size, density, and the associated temperature conditions, were approximately modal for each class of habitat; and a study of development was made in them. The "dense wort," "sparse wort," and "shade" type sites* provided conditions closely resembling those in habitats of classes (i), (ii), and (iii) respectively. In each type site the daily temperature regime was practically identical with that in two study areas of the corresponding class.

The basic procedure used for determination of the mean times taken by the various stages at different temperatures was to place 30 or more newly produced individuals of the stage concerned on moist blotting paper in small, shallow glass dishes. These were covered with a single layer of coarse cheesecloth and set out beneath the mats of *Hypericum* in the type sites where they were kept until the stage ended. In this way individuals were retained within half an inch of their natural situations on the foliage or beneath it. An approximate measure of the mean temperature affecting the eggs and larvae was given by maximum and minimum thermometers placed immediately beside the dishes and covered completely by the *Hypericum* foliage. The moist blotting paper proved to be essential only for the egg stage of each species. It was necessary to moisten the blotting paper at intervals of a few days in order to keep eggs in the same condition as those present on the *Hypericum* plants, i.e. turgid or almost so. The larvae, providing they were fed daily on fresh shoots of *Hypericum,* were not affected appreciably by the absence of moist blotting paper.

IV. GENERAL BEHAVIOUR AND SEASONAL CYCLE

(*a*) *General Behaviour*

(i) *Larval Stage.*—In Australia, as in the northern hemisphere (Wilson 1943; Currie and Garthside 1932), the larval stages of both insects occurred when the autumn-winter growth phase of *Hypericum* was in progress, and lived in close association with the mats of procumbent stems. After hatching, the first-instar larvae moved to the ends of the stems and crawled between the overlapping leaves of the growing tips. Most feeding took place in the early hours of the morning. The young larvae fed mainly on the unopened leaf buds and adjacent soft, immature leaves, crawling from tip to tip. Soon after daybreak most individuals concealed themselves between the end leaves of the stems where they remained during the daylight hours. Occasionally a few were found on the ground near the bases of the plants.

After reaching the second instar the majority of individuals of both species left the plants daily after feeding and collected on and in the damp plant debris beneath the *Hypericum* mats. There, they exhibited a marked tendency to group into clusters, in which individuals of both species and different instars clung together. This habit of clustering appeared to be due to a positive type of gregariousness. Each night these larvae returned to the plants some time after 10.00 p.m.

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* The last-mentioned site differed from the others in being shaded throughout the day by small trees and part of a building.

The occupation of shaded situations by all larvae during the day appeared to result, partly at least, from a positive kinetic response to light. Because of their very small size, the first-instar larvae apparently encountered low enough light intensities to cause a cessation of crawling while they were still on the plants. The more-exposed older larvae continued to crawl until they reached the debris beneath the plants. A few, mainly second-instar larvae, sometimes remained on the plants where they perched with their heads thrust between the leaves and the rear parts of their bodies exposed.

During the entire feeding period and subsequent pupation, the larvae of both species remained close to where they had hatched. When the food supply was exhausted they showed no apparent ability to direct their movements towards food at a distance, and appeared to reach it by wandering in an almost random manner. Few succeeded in reaching food at distances exceeding 10-15 yd.

When the feeding period ended the larvae of both species entered the soil where they formed globular cells less than 2 in. from the surface. They passed through a resting stage in the cells and then pupated. After reaching the adult stage the insects burrowed to the surface and ascended the plants (see also Wilson 1943; Clark and Clark 1952).

(ii) *Adult Stage.*—The adults of both species were, in general, sedentary in habit. The majority of individuals appeared to remain within a few yards of where they had pupated unless the food supply was exhausted or the rare mass flights occurred. Most feeding and movement from plant to plant took place at night. During the spring feeding period, the adult beetles perched on the erect, fertile stems of the weed throughout the day, frequently remaining almost motionless for hours on end. As in the larval stage the adult insects showed a marked tendency to group in clusters.

At the end of the spring feeding period, the adult beetles deserted the plants and took up positions beneath plant debris at the soil surface, where they aestivated. After aestivation ended the adults of each species again ascended the fertile stems of the weed which, by this time, had commenced to dry off and lose their leaves. After exposing themselves daily on the erect stems for approximately four weeks, they retired to the bases of the plants, remaining thereafter in concealment beneath the mats of procumbent stems. Feeding and oviposition occurred at night. Most eggs were laid on the undersurfaces of the leaves (*C. gemellata* particularly) and in the growing tips of the shoots (*C. hyperici* particularly).

Wilson (1943) first recorded the interesting fact that both *C. gemellata* and *C. hyperici* adults fly in Australia, although neither were ever observed to fly in France and England respectively, except in the laboratory. There, flight was observed in sunlight at relatively high temperatures (approximately 104°F.

(40°C.) for *C. gemellata*). During the study period the present author frequently saw adults of *C. gemellata* in flight in the spring and early autumn. Flight by *C. hyperici* was observed only during the spring. In both species the proportion of individuals that took to the wing on spring days appeared to increase as the season advanced and temperatures rose. In general, however, the total percentage of beetles that migrated from an area by flight was undoubtedly low. The exceptions were mass flights from small clearings, surrounded by dense timber, where the temperature became relatively high because of reduced air movement.

In all areas the insects were observed to fly only from positions high on the host plant. After taking off they rose rapidly and fluttered downwind. The distance covered by a single flight was usually much less than 100 yd. After repeated flights over a period of several weeks during the spring of 1949, some adults of both species reached uncolonized stands of *Hypericum* up to a mile from the nearest population of each insect, showing that they had travelled at least this distance. Further observations showed that few individuals travelled more than a few hundred yards during the spring. The observed distances covered by *C. gemellata* during the early autumn were all less than 440 yd. It was thus evident that the insects have only a limited capacity for flight. It has been sufficient, however, to aid materially both in the invasion of new areas and in the recolonization of sites in which the previous occupants had been eliminated.

Observations on the effect of rising high temperatures on the behaviour of adults of *C. gemellata* and *C. hyperici* in the laboratory showed that a state of "nervousness" and relatively great activity occurred at "sun" temperatures over 85°F. (29.4°C.) as measured by ordinary mercury-in-glass thermometers. When in this condition some individuals raised their elytra and attempted to fly. The general behaviour of the beetles resembled that of insects exposed to supraoptimal temperatures (Section IX). Thus it is strongly suspected that flight in *C. hyperici* and *C. gemellata* is symptomatic of uncomfortably high body temperatures.

(*b*) *Seasonal Cycle*

The seasonal occurrence of the immature stages of each species is shown in Table 4, the figures for which were derived from the 1949 population samplings. The results for cleared and timbered areas have been given separately as the rate of development in the latter was slower at the same time of year (see below). Less detailed observations in 1948 and 1950 showed essentially the same pattern of events. The first eggs of *C. gemellata* were laid late in March and the first larvae appeared 1-2 weeks later. Laying by *C. hyperici* did not begin until late April or early May and the first larvae appeared late in June. By the end of the developmental period *C. hyperici* had almost caught up with *C. gemellata*.

To obtain some idea of the total developmental period, following oviposition at different times of the year, batches of 30-50 newly laid eggs of each species were set out in the type sites, and development was allowed to

TABLE 4

MEAN PERCENTAGE COMPOSITION OF POPULATIONS OF *C. GEMELLATA* AND *C. HYPERICI* IN STUDY AREAS CONTAINING ABUNDANT FOOD THROUGHOUT THE SEASON, 1949 (OMITTING PARENT ADULTS)

Species and Stage	Early March	Early April	Late April	Late May	Late June	Mid July	Late August	Late September	Late October	Late November
(*a*) Treeless areas (12 for *C. gemellata,* 10 for *C. hyperici*)										
C. gemellata										
Eggs	0	89	62	35	21	14	2	1	0	0
1st-instar larvae	0	10	8	7	6	5	1	1	0	0
2nd-instar larvae	0	1	7	7	6	6	1	0	0	0
3rd-instar larvae	0	0	11	10	11	11	2	1	0	0
4th-instar larvae	0	0	9	23	16	16	10	7	1	0
Resting 4th-instar larvae	0	0	3	18	40	48	80	20	4	0
Pupae	0	0	0	0	0	0	4	52	22	0
Young adults	0	0	0	0	0	0	0	18	73	100
C. hyperici										
Eggs	0	0	0	100	92	84	30	7	0	0
1st-instar larvae	0	0	0	0	8	14	44	11	1	0
2nd-instar larvae	0	0	0	0	0	2	12	6	1	0
3rd-instar larvae	0	0	0	0	0	0	5	9	3	0
4th-instar larvae	0	0	0	0	0	0	9	29	5	0
Resting 4th-instar larvae	0	0	0	0	0	0	0	29	11	0
Pupae	0	0	0	0	0	0	0	9	40	0
Young adults	0	0	0	0	0	0	0	0	39	100
(*b*) Timbered areas (3 for *C. gemellata,* 5 for *C. hyperici*)										
C. gemellata										
Eggs	0	77	48	33	23	28	16	10	0	0
1st-instar larvae	0	23	14	15	19	25	56	2	2	0
2nd-instar larvae	0	0	8	9	15	13	3	2	0	0
3rd-instar larvae	0	0	21	6	7	14	0	0	0	0
4th-instar larvae	0	0	9	23	16	6	3	16	9	0
Resting 4th-instar larvae	0	0	0	14	15	14	22	51	9	0
Pupae	0	0	0	0	5	0	0	19	27	0
Young adults	0	0	0	0	0	0	0	0	53	100
C. hyperici										
Eggs	0	0	100*	100	96	95	60	18	5	0
1st-instar larvae	0	0	0	0	4	5	40	29	16	0
2nd-instar larvae	0	0	0	0	0	0	0	28	3	0
3rd-instar larvae	0	0	0	0	0	0	0	19	3	0
4th-instar larvae	0	0	0	0	0	0	0	6	19	0
Resting 4th-instar larvae	0	0	0	0	0	0	0	0	50	0
Pupae	0	0	0	0	0	0	0	0	4	0
Young adults	0	0	0	0	0	0	0	0	0	100

* Eggs present in only one area.

continue until the adult stage was reached. During the feeding period the larvae were retained in the egg dishes and fed daily. As soon as the first fourth-instar larva in a dish showed signs of burrowing behaviour, all individuals were transferred to the soil surface beneath the mats of *Hypericum*. There they were retained by a strip of sheet iron, 1½ in. wide, with the ends joined to form a circular enclosure 4 in. in diameter. Each enclosure was driven into the soil to a depth of ½ in., and a piece of cheesecloth was fastened over the top by rubber bands. Food was provided daily until all individuals had entered the soil. The resulting adults were collected as they emerged some time later.

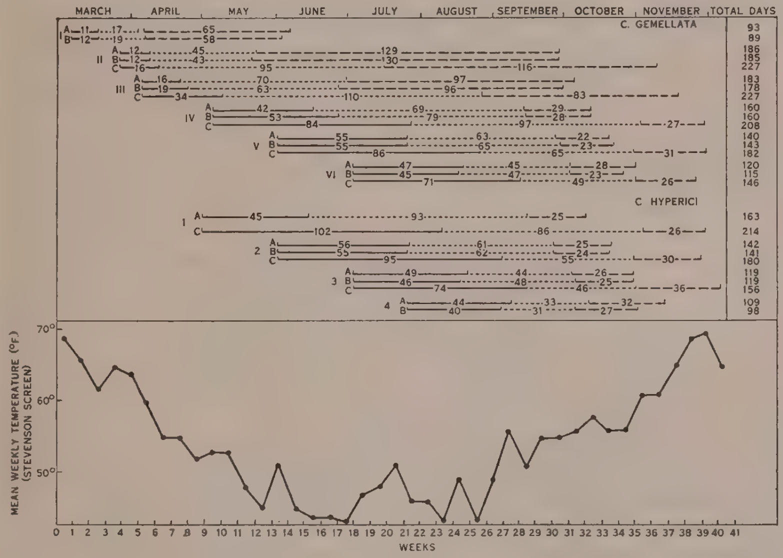

Fig. 1.—Average times taken by batches of *C. gemellata* and *C. hyperici* to complete development from oviposition to adult emergence in the dense wort (*A*), sparse wort (*B*), and shade (*C*) type sites (1950). The accompanying graph shows the seasonal temperature conditions as recorded in a standard thermometer screen.
Solid line: Mean incubation period.
Line of dots: Mean larval feeding period.
Line of dashes: Mean period in pupal cells.

The mean incubation period, mean larval feeding period, and mean period spent by resting larvae and pupae in the soil were computed for each batch and are shown in Figure 1. The accompanying graph gives the seasonal temperature conditions as measured by a thermograph in a standard meteorological screen near the type sites. Beneath the mats of *Hypericum* the mean weekly air temperatures were 2-4°F. higher than in the screen in the dense and sparse wort type sites, and 2-5°F. lower than in the screen in the shade type site.

Newly laid eggs of *C. gemellata*, placed in the dense and sparse wort type sites early in March 1950, produced adults during the winter. These individuals emerged over the same period as did a relatively small number of adults in the field from the few places where oviposition began before mid March. For all other batches of *C. gemellata* adult emergence was delayed until the spring. In the dense and sparse wort sites the first adults from batch II emerged late in September. The emergence of subsequent batches began later, and the total period of development was progressively shorter. By mid November all survivors had reached the adult stage and left the soil. It will be observed that the mean periods of development differed little for the dense wort and sparse wort type sites, although, in general, the daily maximum temperatures were higher and the daily minima lower in the latter (Tables 5 and 6). In the field, emergence began late in September or early in October in similar study areas (in all of which laying began late in March). Complete or almost complete adult emergence took only 2½-3 weeks in each study area. This was due largely to the fact that most eggs in such areas hatched between mid April and mid June.

In the shade type site the adult emergence from corresponding batches began a month or more later than in the other sites. The later batches took less time to complete development in it than the earlier ones, and the whole emergence was distributed over a shorter period than in the other sites. In timbered study areas in the field the adult emergence commenced 2-4 weeks later than in adjacent treeless areas and continued for approximately 2-3 weeks.

The fewer results for *C. hyperici* show the same general pattern. The total period of development was progressively shorter for successive batches in all three sites. The total developmental periods for corresponding batches of the two species differed very little. In the study areas the emergence periods of *C. hyperici* adults were of similar duration to those of *C. gemellata*, but peak numbers occurred about 3 weeks later. This was probably due to the fact that most *C. gemellata* eggs were laid in April and most *C. hyperici* eggs between late May and early July (Section VI). It will be observed that the mean emergence dates indicated in Figure 1 for *C. gemellata* adults, produced from eggs laid between March and early May, preceded those for *C. hyperici* adults, developing from eggs laid early in June and July, by a month or less.

After their emergence in the field the adults of *C. hyperici* and *C. gemellata* fed for 6-8 and 8-12 weeks respectively, and then aestivated. Most individuals of both species began aestivation early in December. The aestivation period of *C. gemellata* adults usually ended late in February or early in March, shortly after the host plant had begun to produce the procumbent foliage on which the eggs are laid. Copulation soon occurred and oviposition began. *C. hyperici* became active again about 6 weeks later and, in most areas, began to oviposit in late April or early May. The males of both species contained what appeared to be mature spermatozoa before aestivation ended.

TABLE 5

MEAN INCUBATION PERIODS FOR EGGS OF *C. GEMELLATA*, 1949-50

Dense Wort Type Site				Sparse Wort Type Site				Shade Type Site			
Date Started	Mean Daily Temperature (°F.) (approx.)	Mean Daily Temperature Range (°F.) (approx.)	Mean Time to Complete Development to Eclosion and Standard Error (days)	Date Started	Mean Daily Temperature (°F.) (approx.)	Mean Daily Temperature Range (°F.) (approx.)	Mean Time to Complete Development to Eclosion and Standard Error (days)	Date Started	Mean Daily Temperature (°F.) (approx.)	Mean Daily Temperature Range (°F.) (approx.)	Mean Time to Complete Development to Eclosion and Standard Error (days)
6.iv.1949	54	34	27.24 ± 0.42	20.v.1949	44	24	65.12 ± 0.64	21.v.1949	44	10	95.48 ± 3.01
20.v.1949	44	20	63.93 ± 1.15					5.vi.1949	44	10	97.04 ± 1.44
21.v.1949	44	21	61.82 ± 1.85								
5.vi.1949	44	21	64.01 ± 2.18								
22.ii.1950	72	32	8.76 ± 0.13	22.ii.1950	72	32	9.12 ± 0.16	22.ii.1950	63	22	11.50 ± 0.15
15.iii.1950	68	24	9.92 ± 0.22	15.iii.1950	70	34	10.56 ± 0.36	15.iii.1950	61	15	14.83 ± 0.17
21.iii.1950	67	21	10.81 ± 0.18	21.iii.1950	69	29	10.88 ± 0.25	21.iii.1950	61	16	14.14 ± 0.24
28.iii.1950	64	17	12.03 ± 0.18	28.iii.1950	64	27	11.80 ± 0.21	28.iii.1950	57	16	16.17 ± 0.36
6.iv.1950	58	29	15.50 ± 0.46	6.iv.1950	58	38	18.53 ± 0.61	6.iv.1950	49	20	34.00 ± 0.90
14.iv.1950	56	32	22.23 ± 0.27	14.iv.1950	55	37	25.59 ± 0.54	14.iv.1950	46	17	52.05 ± 0.35
6.v.1950	49	27	42.18 ± 0.70	6.v.1950	48	32	52.66 ± 0.92	6.v.1950	43	15	84.00 ± 0.69
2.vi.1950	48	24	54.92 ± 0.55	2.vi.1950	48	32	54. 54 ± 0.92	2.vi.1950	43	15	85.97 ± 0.73
4.vii.1950	49	22	47.15 ± 0.65	4.vii.1950	50	32	45.36 ± 0.95	4.vii.1950	45	15	71.38 ± 0.61

TABLE 6

MEAN INCUBATION PERIODS FOR EGGS OF *C. HYPERICI*, 1949-50

Dense Wort Type Site				Sparse Wort Type Site				Shade Type Site			
Date Started	Mean Daily Temperature (°F.) (approx.)	Mean Daily Temperature Range (°F.) (approx.)	Mean Time to Complete Development to Eclosion and Standard Error (days)	Date Started	Mean Daily Temperature (°F.) (approx.)	Mean Daily Temperature Range (°F.) (approx.)	Mean Time to Complete Development to Eclosion and Standard Error (days)	Date Started	Mean Daily Temperature (°F.) (approx.)	Mean Daily Temperature Range (°F.) (approx.)	Mean Time to Complete Development to Eclosion and Standard Error (days)
20.v.1949	44	20	70.02 ± 2.04	19.v.1949	44	24	76.50 ± 0.41				
21.v.1949	44	21	76.94 ± 1.26					21.v.1949	44	11	105.95 ± 2.84
5.vi.1949	44	21	71.98 ± 1.50					5.vi.1949	44	11	100.51 ± 2.14
1.v.1950	50	29	44.57 ± 2.36					1.v.1950	44	16	101.93 ± 1.14
2.vi.1950	48	24	56.17 ± 0.42	2.vi.1950	48	32	55.45 ± 0.37	2.vi.1950	43	15	94.55 ± 0.49
4.vii.1950	49	23	48.82 ± 0.64	4.vii.1950	50	32	46.46 ± 0.60	4.vii.1950	45	15	74.21 ± 0.53
27.vii.1950	50	27	44.17 ± 0.25	27.vii.1950	52	37	40.25 ± 0.29	27.vii.1950	46	16	61.38 ± 1.08
22.viii.1950	54	30	27.73 ± 0.36	22.viii.1950	56	41	26.77 ± 0.51	22.viii.1950	48	18	45.80 ± 0.19

V. Factors Affecting the Rate of Egg Development

As discussed in Section VI, a knowledge of the approximate incubation periods of eggs laid at different times was necessary for estimation of the total egg production of each species in the study areas. It was also essential to know whether or not temperature was the only factor of importance affecting the rate of development. In this section the effects of temperature and desiccation are considered briefly.

(*a*) *Effect of Temperature*

The mean times taken by batches of 30-120 turgid eggs to complete development during 1949 and 1950 in the type sites, together with the associated mean daily temperatures and mean daily temperature ranges, are shown in Tables 5 and 6. The daily temperature fluctuations were greatest in the sparse wort type site and least in the shade type site. The results for 1950 cover a longer total interval for each species than its normal oviposition period in the field.

In general terms, the results show that the length of the incubation period is related to temperature in the usual way. The differences in the mean times taken by the eggs of both species are, for the most part, small for corresponding batches in the dense and sparse wort type sites, indicating that the developmental rates were not affected much by the substantial differences occurring in the amount of overlying foliage. In the shade type site development was slower for corresponding batches than in the other sites.

To compare the rates of egg development at similar mean temperatures, but differing maxima and minima, the reciprocal of mean time of development was plotted against mean temperature for each type site. At similar mean temperatures, the mean daily rates of both species were, on an average, highest in the site in which temperature fluctuated least and lowest in that in which temperature fluctuated most. The main exceptions were the figures for 1949 winter eggs. Further work, including a rough estimation of the developmental zero for eggs of each species, indicated that the observed site differences in rate of development at apparently similar mean temperatures were due to three factors:

(i) Curvelinearity in the underlying relationship between temperature and rate of development.

(ii) Differences in the periods spent by eggs at temperatures below and just above 38.5°F., the estimated developmental zero for both species.

(iii) Inaccuracies in the estimation of mean temperature.

The graphs of mean daily rate of development on mean daily temperature showed that, at temperatures in the vicinity of 44°F., the rate of development of *C. hyperici* eggs was lower than that of *C. gemellata* eggs in all three type sites. Around 48°F. the differences between their rates of development were smaller. Above 48°F. the corresponding regression lines diverged, development in *C. gemellata* eggs becoming increasingly more rapid than in *C. hyperici* eggs with increase in temperature.

The *C. gemellata* data for all three sites were pooled and grouped on the basis of mean temperature (classes of 5°F.). A sigmoid curve was obtained when the group mean daily rates of development were plotted against the group mean daily temperatures. The course described by the six points approximated closely to that of a Verhulst-Pearl logistic curve described by the formula

$$\frac{100}{y} = \frac{12.4900}{1 + e^{(8.35959 - 0.141271\,x)}}$$

where y is the time in days for eggs to complete development to eclosion at a mean temperature x°F., and e is the base of the Napierian system of logarithms*. The result is of interest as Davidson (1944) has demonstrated that curves of this type describe very accurately the relationship between temperature and rate of development of insect eggs at constant temperatures. The data for *C. hyperici* were too few for grouping. The same kind of overall relationship is probable on the basis of similarity in the observed trends.

TABLE 7

MEAN TIMES TAKEN BY EGGS TO COMPLETE DEVELOPMENT IN THE "WET" AND "DRY" TREATMENTS (4 REPLICATES OF 25-30 EGGS)

No. of Experiment	Species	Mean Time from Oviposition to Eclosion (days)		Approximate Conditions	
		Dry Treatment	Wet Treatment	Mean Temperature All Batches (°F.)	Mean Saturation Deficit (dry treatments)
1	*C. gemellata*	12.24	11.02	68	0.17
2	*C. gemellata*	12.58	10.92	66	0.13
3	*C. gemellata*	60.53	55.17	47	0.08
	C. hyperici	62.17	62.83	47	0.08

(*b*) *Effect of Desiccation*

Several simple tests were carried out in the laboratory to ascertain if dry conditions and consequent loss of water from the eggs of *C. gemellata* and *C. hyperici* affected the time taken from oviposition to eclosion. The developmental periods were compared for eggs kept in a saturated atmosphere (just above water surfaces in closed containers) and eggs kept at ordinary room humidities (in similar containers without lids and water). No attempt was made to control temperature. The daily temperature range differed little from that occurring beneath the mats of *Hypericum* in the dense wort type site. The relative humidities affecting the exposed eggs and the temperatures affecting all eggs were measured crudely by a thermohygrograph around which the egg batches were placed, replicates of the "wet" treatment alternating with those of the "dry" treatment. The results are summarized in Table 7.

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* For each of the six observed values for mean daily rate of development the deviation from the corresponding value computed from the formula of the curve lay within the range of 0.78 and 6.47 per cent. of the calculated value.

The saturation deficits to which the eggs in the dry treatments were exposed must have been much higher during the day than those occurring in the type sites and in the field at the time (relative humidity approximately 100 per cent. in all places at night). Unlike the eggs in the wet treatments and those out of doors, which remained turgid or nearly so, the individuals in the dry treatments all lost water rapidly and collapsed partially. So much water was lost that the larvae produced were little more than half the normal length. In spite of these abnormally dry conditions, the *C. gemellata* eggs took only from 10 to 15 per cent. longer to complete development than those in the wet treatments. The longer incubation periods appeared to be due partly to slower development and partly to the relatively long time taken by the undersized larvae to burst the chorion and escape. In the single experiment for which eggs of *C. hyperici* were available, and included in the same dishes as *C. gemellata,* only four eggs hatched out of 100 subjected to dry conditions. These took approximately the same average time as those in the wet treatments.

A further test was made in which the dry treatment was modified. Eggs of both insects were kept at the prevailing atmospheric saturation deficits only from 9.00 a.m. to 5.00 p.m. and transferred to moisture conditions identical with those in the wet treatments for the remaining hours each day. Altogether, 68 per cent. of the *C. gemellata* eggs and 55 per cent. of the *C. hyperici* eggs exhibited slight crumpling due to water loss. The mean time of development of these individuals was almost identical with that of eggs remaining turgid.

In samples collected from the study areas, the proportion of individuals exhibiting slight crumpling, similar to that observed in the fourth test, never exceeded 30 per cent. and was generally less than 5 per cent. Fertile eggs, collapsed to the extent observed in the first three tests, were very rare — less than 2 per cent. in any sample. It was concluded that very few eggs had their rate of development affected appreciably by water loss under natural conditions.

VI. SURVIVAL AND THE FAVOURABLENESS OF DIFFERENT HABITATS

(*a*) *Estimation of Egg Numbers in the Field*

In order to study the survival of the beetles, and to compare the favourableness of the principal types of habitat to them, it was necessary to estimate the total seasonal egg production of each species in the study areas. Both species oviposited nightly for some weeks. Eggs of *C. gemellata* began to hatch in large numbers long before laying ceased, whereas relatively few eggs of *C. hyperici* hatched before the oviposition period ended. Basically, the problem was to estimate the numbers of eggs added during some or all of the intervals between population samplings made on selected dates spaced throughout the oviposition period of each insect. The periods between successive population counts were chosen so that eggs of either species, laid immediately before one count, would not have sufficient time to complete development to eclosion before the next count was made.

The results for a representative selection of the study areas, given in Table 8, show the observed differences in the seasonal occurrence of eggs of each insect, and the total production. It will be observed that eggs of *C. gemellata* were most plentiful during the autumn and early winter, whereas those of *C. hyperici* were most numerous during the winter. In both 1949 and 1950 few recently laid eggs of *C. gemellata* were found after mid May, showing that oviposition had almost ceased by the end of the autumn. In 1949, *C. hyperici* eggs were not found until May except in the forest area 3*c*. Re-

TABLE 8

MEAN NUMBER OF *CHRYSOMELA* EGGS PER SQ. LK. FOR VARIOUS STUDY AREAS, AND TOTAL EGG PRODUCTION PER SQ. LK.

(All *C. gemellata* figures for early April include a few larvae as do the *C. hyperici* figures for July 1949)

Study Area	Sampling No.							Total Eggs Produced and Standard Error of Estimate
	I Early April	II Late April	III Late May	IV Late June	V Mid July	VI Late August	VII Late Sept.	
1949 *C. gemellata*								
Dense wort (treeless)								
1*a*	1.83	2.11	2.27*	0.11*	0.02	0.00	0.00	4.08 ± 0.73
2*a*	4.78	4.96	3.80*	2.07*	0.56*	0.00	0.00	9.49 ± 1.16
3*a*	4.41	5.56	2.06*	1.95*	2.65*	0.14	0.00	11.35 ± 1.62
4*a*	6.54	4.81	1.59*	1.09*	1.10*	0.17	0.10	11.46 ± 1.63
5*a*	7.53	1.67	1.97	0.36	0.64	0.22	0.00	9.81 ± 0.92
Sparse wort (treeless)								
1*b*	3.74	3.01	0.86*	0.09*	0.01	0.00	0.00	5.01 ± 0.63
2*b*	5.90	3.33	0.42*	0.54*	0.28	0.03	0.00	7.33 ± 1.06
3*b*	1.48	0.81	0.10	0.10	0.05	0.00	0.00	1.79 ± 0.20
4*b*	0.67	0.60	0.37*	0.06*	0.00	0.00	0.00	1.06 ± 0.35
5*b*	1.57	1.06	0.85*	0.06*	0.01	0.00	0.00	2.44 ± 0.44
Eucalypt forest								
1*c*	0.94	0.63	0.68*	0.06*	0.01	0.01	0.00	0.96 ± 0.21
Pine plantation								
2*c*	0.85	0.59	0.49*	0.17*	0.25	0.06	0.01	1.04 ± 0.41
1949 *C. hyperici*								
Dense wort (treeless)								
1*a*	0.00	0.00	1.23*	1.53*	2.69	0.05	0.00	2.69 ± 0.57
2*a*	0.00	0.00	3.13*	5.36*	6.20*	0.67	0.04	6.20 ± 1.53
4*a*	0.00	0.00	0.74*	2.35*	3.56*	0.40	0.07	3.56 ± 0.84
Sparse wort (treeless)								
2*b*	0.00	0.00	0.47*	1.49*	1.84	0.14	0.04	1.84 ± 0.48
4*b*	0.00	0.00	1.26*	2.42*	3.17	0.30	0.01	3.17 ± 0.46
5*b*	0.00	0.00	0.09*	0.07*	0.65	0.01	0.01	0.65 ± 0.11

TABLE 8 (*Continued*)

Study Area	Sampling No.							Total Eggs Produced and Standard Error of Estimate
	I Early April	II Late April	III Late May	IV Late June	V Mid July	VI Late August	VII Late Sept.	
Eucalypt forest								
1*c*	0.00	0.00	0.85*	0.37*	0.35	0.06	0.00	0.85 ± 0.23
3*c*	0.00	0.36	2.40	1.92	1.34	0.53	0.07	2.40 ± 0.61
Pine plantation								
2*c*	0.00	0.00	1.23*	3.59*	9.56	4.22	0.15	9.56 ± 1.82
4*c*	0.00	0.00	0.43*	1.11*	1.37	0.27	0.00	1.37 ± 0.23
1950 *C. gemellata*								
Dense wort (treeless)								
8*a*	3.30	2.71	1.01	0.62	0.06	—	0.00	6.56 ± 0.41
9*a*	4.91	1.96	0.91	0.03	0.00	—	0.00	7.71 ± 0.66
10*a*	5.84	0.59	0.23	0.53	0.11	—	0.00	6.36 ± 0.56
11*a*	2.48	2.29	1.91	1.30	0.13	—	0.00	4.99 ± 0.61
12*a*	1.88	2.90	0.85	0.23	0.18	—	0.00	4.98 ± 0.39
13*a*	4.76	1.20	0.14	0.00	0.00	—	0.00	5.64 ± 0.46
Sparse wort (treeless)								
3*b*	5.94	1.39	0.11	0.00	0.00	—	0.00	7.38 ± 0.34
Eucalypt forest								
1*c*	3.24	0.41	0.28	0.20	0.00	—	0.00	3.29 ± 0.21
1950 *C. hyperici*								
Dense wort (treeless)								
8*a*	0.00	0.48	2.10	2.25	0.40	—	0.00	2.34 ± 0.26
9*a*	0.00	0.08	1.73	0.64	0.55	—	0.00	1.91 ± 0.18
10*a*	0.00	1.15	0.51	3.86	1.10	—	0.00	5.39 ± 0.31
11*a*	0.00	1.03	9.30	4.66	1.00	—	0.00	9.86 ± 0.84
12*a*	0.00	2.13	21.70	—	7.06	—	0.00	26.01 ± 0.95

The 1950 population counts were made 1-2 weeks later than in 1949.

* Statistical method used to identify eggs, consequently the estimate has a substantial error of identification associated with it (see Section II).

cently laid eggs were very scarce after early July, showing that oviposition practically ceased during midwinter. In 1950 oviposition by *C. hyperici* began approximately 2-3 weeks earlier than in 1949, and in several places (not including any study areas) a few recently laid eggs were found as late as August 20.

Three procedures were used for determination of the approximate total egg production of the beetles. Data on time of egg development in the three type sites were used to estimate the periods necessary for eggs to complete development to eclosion in corresponding study areas. While simple in principle the methods were complicated in practice. They are now described briefly, full details being given in Appendix II.

The first method depended on estimation of the minimum period for all eggs present on a particular count date to complete their development. This amounted to estimating the median incubation period of eggs laid the night before the count date. The eggs present in a study area at the end of this period were assumed to have been laid during the period. The first step was to construct a curve of egg numbers on time from the results of the population counts made in the area. Then, using temperature-development data

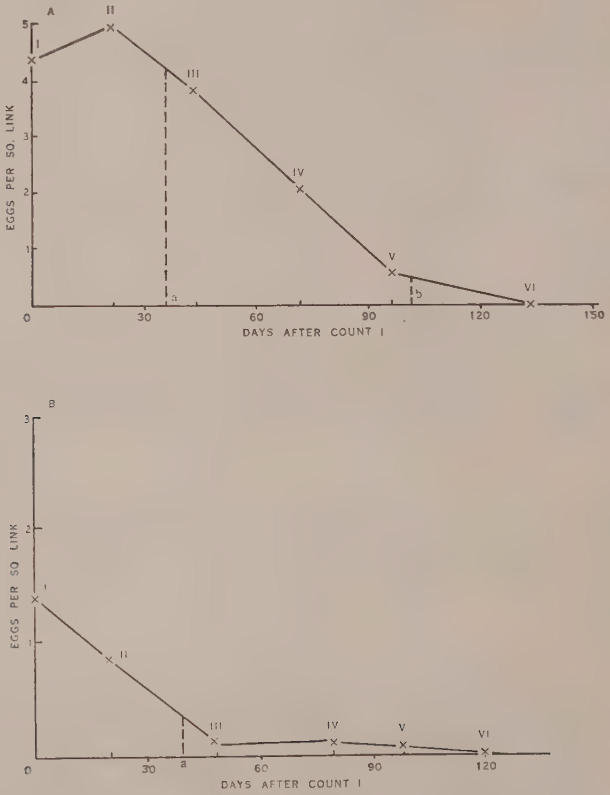

Fig. 2.—Curves showing the numbers of *C. gemellata* eggs in: *A*, a study area resembling the dense wort type site; *B*, a study area resembling the sparse wort type site.
Egg counts and sampling dates are indicated by I-VI. In each diagram *a* is the estimated median hatching date for eggs laid the night before count I, and intercept *a* indicates the number of eggs laid during the interval between count I and *a*. In *A*, *b* is the estimated median hatching date for eggs laid the night before *a*, and intercept *b* shows the approximate number of eggs laid during the interval between *a* and *b*. No eggs were laid after *a* in area *B*.

from the appropriate type site in combination with records of mean daily temperature, an estimate was made of the period necessary for all the eggs present on the date of the first count to complete development. The number of eggs present on the estimated hatching date, i.e. the number added during the time interval, was obtained by interpolation on the curve (Fig. 2). Using this estimated hatching date as the next starting point the process was repeated, the second interpolation providing an estimate of the number of eggs laid during the second interval. The total number of eggs was obtained by adding the numbers present at the end of each interval to the number present on the date of the first population count.

In addition to errors involved in using data from the type sites to interpret events in the field, this procedure contains an unmeasurable error due to the fact that the hatching of eggs laid on a particular night took several days for completion. However, some eggs laid just before and just after these eggs hatched on their median hatching date. As the errors involved would generally have been small, it was assumed that such individuals compensated exactly for the incomplete hatch of the first-mentioned eggs on the date concerned.

This method was used for *C. gemellata* in 1949. Sampling errors due to spatial distribution and identification were estimated for each sampling date and hence for the successive dates of completion of hatching, assuming no errors in these dates and linear changes between dates of observation. The individual variances were accumulated to give the approximate variance of total egg production.

The estimation of egg production by *C. hyperici* in 1949 was a much simpler matter because hatching began either shortly before or after laying ceased. The total egg production was estimated as the total number of individuals present when laying ceased, as a few larvae had hatched in most areas. A small proportion of the eggs in each study area would have been dislodged from the plants by this time and therefore missed (Section IX). However, the proportion missed appeared to be similar for all but two study areas in which the losses were negligible (see Appendix II). It was assumed that 10 per cent. were missed in the others and the appropriate correction was applied before using the figures in the computation of survival rates. It was found to have no material effect on the results. The variance of total egg production was composed of the variances due to spatial distribution of eggs and larvae, and that of egg identification when the statistical method of separation was employed (Section II). The results given in Table 8 (for both 1949 and 1950) are not corrected for egg dislodgment.

The third procedure depended on estimation of the number of eggs for each count that would still be present as unhatched individuals on the date of the next count. A random sample of approximately 250 eggs of each species was collected from the immediate vicinity of each study area on the date of each count. (Collection from the areas themselves would have caused artificial reductions of the population.) The eggs were set out in the usual way in the corresponding type site. The number of unhatched, uncollapsed individuals present on the date of the next count was recorded and calculated as a proportion of the total eggs in the sample*. It was assumed that the proportion of unhatched, uncollapsed individuals was similar for the corresponding count made in the study area and the approximate number of residual eggs was computed. This estimated residue subtracted from the total number of eggs present on the date of the next count provided an estimate of the number added during the interval between the counts. The estimates of egg numbers added during successive intervals were added to the number present on the date of the first population count to give the total production.

This method was used for both species in 1950. A correction allowing for an error of 10 per cent. due to dislodgment was applied to each result for *C. hyperici* before using it in the estimation of survival rates. The variances due to spatial distribution and estimation of the proportional hatch were accumulated to give the variance of total egg production. As all eggs were allowed to complete development to eclosion after collection, the errors of identification were negligible (Section II). As in the first procedure, the estimates given by this method contained an unmeasurable error due to use of the type sites in the manner described.

A careful examination of the first and third techniques, in relation to all observations made on the egg stage, indicated that their inherent defects were almost negligible in comparison with the large errors associated with field sampling and identification by the statistical method for which due allowance could be made. As mentioned in Section III, the 1 per cent. level was taken as the minimum for significant differences, instead of the more frequently used 5 per cent. level, to allow for the approximate nature of these egg estimates in the individual comparisons which follow.

(*b*) *Survival for the Period from Oviposition to Adult Emergence*

(i) *In Treeless Areas.*—The estimated survival rates of each species for the period from oviposition to adult emergence are shown in Table 9 together with the mean amounts of ground cover present throughout the period. In each study area the total amount of ground cover remained almost constant throughout the winter and then increased during the spring. The relative amounts of cover for the areas remained almost the same throughout the whole period. It will be observed that the survival of *C. gemellata* was less than 50 per cent. in all sites, and that of *C. hyperici* was less than 60 per cent., approximately.

As some study areas contained much more vegetation than others, consideration was given to the possibility of a relationship between survival and the amount of ground cover present. The data for 1949 and 1950 were pooled†,

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* This residue of eggs was composed entirely or almost entirely of fertile individuals. The majority of infertile eggs collapsed and shrivelled soon after laying, as in the field, where they generally disappeared from the plants 2-3 weeks after oviposition (Section VIII). Such individuals, if present in the samples, were not recorded as unhatched eggs as they would not have been present when the next count was made.

† Areas 3*b* and 1*c* (a timbered site, see Table 10) were the only sites used in both years. In each the survival of *C. gemellata* was similar in 1949 and 1950. This link justified pooling of the data for both years. Area 8*a* was invaded and trampled heavily by cattle at one period and was therefore omitted from the analysis.

TABLE 9

SURVIVAL RATES OF *C. GEMELLATA* AND *C. HYPERICI* FROM OVIPOSITION TO ADULT EMERGENCE IN TREELESS STUDY AREAS, WITH MEAN AMOUNT OF GROUND COVER PRESENT

	Mean Ground Cover (air-dry wt.—g. per 3 by 3 lk.)			Survival				
				C. gemellata		*C. hyperici*		
Area and Year	Amount of Wort	Other Cover (mainly debris)	Total Ground Cover	Survival Rate	Variance	Survival Rate	Variance	Significance of Differences
11*a* (1950)	22	231	253	0.451	0.005580	0.124	0.000310	$P < 0.001$
7*a* (1949)	18	101	119	0.328	0.006975	0.142	0.000841	N.s.*
5*a* (1949)	12	98	110	0.419	0.007955	—	—	—
10*a* (1950)	25	81	106	0.312	0.002013	0.132	0.000326	$P < 0.001$
12*a* (1950)	17	65	82	0.337	0.001753	—	—	—
6*a* (1949)	17	58	75	0.133	0.000497	0.189	0.005773	N.s.
3*a* (1949)	14	60	74	0.488	0.006171	0.208	0.004176	$P < 0.01$
9*a* (1950)	22	51	73	0.178	0.000552	0.582	0.013468	$P < 0.001$
4*a* (1949)	20	45	65	0.140	0.000433	0.146	0.001580	N.s.
13*a* (1950)	14	39	53	0.033	0.000130	—	—	—
1*b* (1949)	4	45	49	0.076	0.000389	0.000	0.000	$P < 0.01$
2*a* (1949)	13	31	44	0.124	0.000776	0.242	0.004659	N.s.
3*b* (1950)	5	37	42	0.253	0.000696	—	—	—
1*a* (1949)	9	28	37	0.245	0.002349	0.017	0.000078	$P < 0.001$
2*b* (1949)	6	31	37	0.108	0.000586	0.168	0.002334	N.s.
3*b* (1949)	4	31	35	0.248	0.004603	—	—	—
4*b* (1949)	1	6	7	0.000	0.000000	0.042	0.000139	$P < 0.01$
5*b* (1949)	2	4	6	0.076	0.000291	0.068	0.000423	N.s.
8*a*† (1950)	20	75	95	0.124	0.000499	0.092	0.000297	N.s.

* Not significant.

† Invaded and trampled by cattle.

and a regression analysis was made. For *C. gemellata* the regression of survival (Y) on total ground cover (X) was expressed satisfactorily by the linear relationship $Y - 0.2194 = 0.001783(X - 70.39)$, the regression coefficient being significant at the 1 per cent. level. Thus, in treeless areas with an adequate food supply, the survival of this insect apparently depended on the total amount of ground cover present. The results for *C. hyperici* gave no suggestion of a similar relationship.

An explanation of the difference between the species was provided by direct observations and the population counts. As discussed later (Section IX), winter temperatures had a similar general effect on the larvae of each species. The amount of cover available appeared to be of similar importance to both chrysomelids during the winter of 1949. However, as a result of high rainfall, their survival rates diverged markedly in some study areas during the following spring when most individuals were in the prepupal and pupal stages. In well-drained areas the spring survival rates were not very different; but, in the more low-lying sites (1*a*, 4*a*, 6*a*, and 7*a*), *C. hyperici* suffered heavy losses as a result of repeated flooding of the pupal cells whereas *C. gemellata* escaped lightly. The differential mortality may be attributed to the earlier emergence of *C. gemellata* from the soil, which enabled it to miss the full impact of the wet conditions. The situation was similar in 1950 (Section IX). Thus, in both years, the spring losses suffered by *C. hyperici* in some dense wort habitats outweighed the protective effects of cover.

For the 1949 study areas (10) in which both insects were present, the mean survival rates of *C. gemellata* and *C. hyperici* for the period from oviposition to adult emergence were 0.172 and 0.122 respectively. The mean difference was not significant when the variance of unweighted differences was used as error. For the 1950 study areas (4) the corresponding results were 0.266 for *C. gemellata* and 0.233 for *C. hyperici*, and again the mean difference was negligible. In both cases the variance of the total of the unweighted differences (given by the product of the number of differences and the variance of the unweighted differences) greatly exceeded the sum of the variances of the individual differences. This means either that the variances of egg or adult numbers, or both, were grossly underestimated or that there was a highly significant interaction between species and sites. The available evidence indicates that due allowance was made for most of the experimental error. Consequently, as the species were undoubtedly affected in a different way, quantitatively, by site differences in association with weather conditions, it was concluded that the above variance differences were due largely to interaction.

The results of the individual comparisons are given in Table 9. In 1949, the survival of *C. gemellata* was higher than that of *C. hyperici* in three areas (1*a*, 3*a*, and 1*b*) and lower in one (4*b*). The difference was negligible elsewhere. In 1950, the survival of *C. gemellata* was higher than that of *C. hyperici* in two areas (10*a* and 11*a*), lower in one (9*a*), and similar in the other. These results conformed with general observations made over much more extensive areas in both years. It was concluded that, although the mortality of the species differed markedly in some treeless sites, their average survival rates were not very different where plenty of food was available to both.

(ii) *In Timbered Areas.*—Table 10 gives the survival rates for *C. gemellata* and *C. hyperici* in pairs of timbered sites and adjacent clearings for the period from oviposition to adult emergence. The survival rates of *C. gemellata* in areas 1*c* (1949 and 1950) and 4*c* were lower than those in the adjacent treeless areas ($P < 0.01$). The difference between the survival rates in areas 2*c* and 2*b* was negligible. Areas 3*a*, 7*a*, and 8*a* were dense wort habitats, whereas 2*b* was of the sparse wort type. Thus the few results suggest that the survival of *C. gemellata* in timbered areas was probably lower than in nearby treeless areas of dense wort, but not very different from that in sites bearing a relatively sparse growth of the weed.

TABLE 10

SURVIVAL RATES FOR *C. GEMELLATA* AND *C. HYPERICI* IN TIMBERED AREAS AND NEARBY CLEARINGS

	Timbered Areas				Treeless Areas				
Study Area	Survival *C. gemellata*	Variance	Survival *C. hyperici*	Variance	Study Area	Survival *C. gemellata*	Variance	Survival *C. hyperici*	Variance
1949									
1*c*	0.013	0.000048	0.000	0.000	7*a*	0.328	0.006975	0.142	0.000841
2*c*	0.262	0.012857	0.041	0.000136	2*b*	0.108	0.000586	0.168	0.002334
4*c*	0.163	0.003265	0.010	0.000040	3*a*	0.488	0.006171	0.208	0.004176
3*c*	—	—	0.004	0.000004	1*a*	0.245	0.002349	0.017	0.000078
5*c*	—	—	0.046	0.000157	2*a*	0.124	0.000776	0.242	0.004659
1950									
1*c*	0.002	0.000002	—	—	8*a*	0.124	0.000499	0.092	0.000297

Areas 2*c* and 4*c* were in pine plantations, the others in eucalypt forest.

The survival rate of *C. hyperici* was less than 5 per cent. in all timbered areas, and consistently lower than in nearby clearings. The t test showed that the mean difference between the survival rates in the two types of site was significant at $P < 0.02$. Comparisons between the survival rates of the two species were limited to areas 1*c*, 2*c*, and 4*c* (1949). The difference was really substantial only in area 4*c* ($P < 0.01$). The data are too few to permit a generalization.

(*c*) *Survival During the Aestivation Period*

Preliminary observations made in the summer of 1948-49 indicated that the mortality occurring during aestivation was high almost everywhere for both insects. The relative numbers of dead and living individuals found at the end of the aestivation period of each species suggested that the survival rate was high only in timbered areas that contained accumulations of leaf litter several inches deep. In spite of a "dislike" of timbered areas (see next section) both *C. gemellata* and *C. hyperici* survived the summer as well or better in them than elsewhere.

To investigate these losses further population counts were made the following summer in small study areas differing in the amounts of debris and other cover present. Sites 1-3 and 7-14 (Table 11) were distributed along the floor of the Ovens Valley, whereas sites 4-6 were on neighbouring hillsides. The first sampling was made as the adults of both species were going into aestivation, 50 per cent. or more of each having entered the debris around the bases of the *Hypericum* plants. The second count for each species was made just before aestivation ended, i.e. mid February for *C. gemellata* and early April for *C. hyperici*.

TABLE 11

SURVIVAL OF *C. GEMELLATA* AND *C. HYPERICI* AT END OF THE AESTIVATION PERIOD, 1949-50

	Mean Amount of Cover: (air-dry wt.—g. per 9 sq. lk.)				Population Density of Beetles per 9 sq. lk. (mean and standard error)			
	1	2	3		1 Start of Aestivation		2 End of Aestivation	
Site	Herbs and Grasses	Debris	Total	Tree Shade: P—present A—absent	*C. gemellata*	*C. hyperici*	*C. gemellata*	*C. hyperici*
1	64	41	105	A	4.3 ± 0.7	1.6 ± 0.3	0.4 ± 0.1	0.2 ± 0.05
2	56	55	111	A	5.0 ± 0.8	2.2 ± 0.8	0.3 ± 0.1	0.3 ± 0.1
3	62	80	142	A	12.8 ± 2.3	12.4 ± 5.3	0.3 ± 0.1	0.7 ± 0.2
4	6	188	194	P	1.9 ± 0.5	2.4 ± 0.4	1.3 ± 0.4	1.0 ± 0.3
5	4	159	163	P	55.3 ± 4.0	13.7 ± 1.0	0.4 ± 0.1	1.4 ± 0.3
6	9	118	127	P	—	6.8 ± 2.1	—	0.7 ± 0.1
7	40	18	58	P*	2.6 ± 0.5	3.8 ± 0.8	0.7 ± 0.2	0.5 ± 0.1
8	17	5	22	P†	2.4 ± 0.9	4.4 ± 0.9	0	0
9	41	1	42	A	2.9 ± 0.5	32.9 ± 4.7	0	0
10	29	7	36	A	0.6 ± 0.2	2.0 ± 0.4	0	0
11	14	16	30	A	45.8 ± 7.6	5.8 ± 0.7	0	0
12	6	10	16	A	—	0.4 ± 0.1	—	0
13	14	15	29	A	1.3 ± 0.2	—	0	—
14	38	16	54	A	0.4 ± 0.1	—	0	—

* Shaded from before noon until sunset.

† Shaded during early morning only.

The details are summarized in Table 11, which gives the mean amount of cover present in each area during the aestivation period of *C. gemellata* (it may be assumed to be similar for *C. hyperici*). As all insects were not actually in a state of aestivation when the first count was made, it cannot be taken for granted that the decreases were due entirely to mortality. However, migration had undoubtedly almost ceased. In the areas lacking trees, survival occurred only where the amounts of plant debris and herbaceous cover were relatively high, particularly the former. In these sites (1-3) the mortality of both insects was high. Some living beetles were found in four of the five areas containing trees. The exception was site 8, which contained very little debris and was not shaded by trees during the hottest part of the day. The survival rate of each species appeared to be highest in site 4, which contained the greatest amount of ground cover.

Although no counts were made therein, the other study areas (1*a*, 2*a*, etc.) were also searched carefully for living beetles at the end of the aestivation periods. Low numbers were present in all dense wort areas and three timbered areas. Only dead individuals were found in the sparse wort areas 1*b*-5*b*. It was concluded that a relatively large body of plant cover, particularly debris, was necessary for the survival of both species during the aestivation period.

(*d*) *Migration from Timbered Areas Before and After Aestivation*

The adults of both species exhibited a marked tendency to avoid occupying timbered sites. They entered forests and plantations in large numbers only during the spring feeding period after the available food in adjacent clearings had been exhausted. Although the numbers of both species so driven into timbered areas were frequently very high, the resulting population densities of *C. gemellata* were nearly always very low for the following generation, whereas those of *C. hyperici* varied greatly.

TABLE 12

POPULATION CHANGES IN ADULT *C. GEMELLATA* AND *C. HYPERICI* DURING THE TWO WEEKS PRIOR TO AESTIVATION IN TIMBERED AREAS AND CLEARINGS (1949)

	Mean Population Density (per 3 × 3 lk.)					
	C. gemellata			*C. hyperici*		
Study Area	Before Aestivation	At Aestivation	Significance of Difference	Before Aestivation	At Aestivation	Significance of Difference
Treeless						
3	18.0	12.8	$P < 0.01$	27.1	12.4	$P < 0.05$
9	1.8	2.9	$P < 0.01$	37.0	32.9	N.s.
10	0.7	0.6	N.s.	2.9	2.0	N.s.
11	44.0	45.8	N.s.	5.5	5.8	N.s.
Timbered						
4	26.2	1.9	$P < 0.001$	4.6	2.4	$P < 0.01$
5	92.2	55.3	$P < 0.01$	11.2	13.7	N.s.
7	17.2	2.6	$P < 0.001$	2.8	3.8	N.s.
8	8.7	2.4	$P < 0.01$	1.9	4.4	$P < 0.01$

To investigate the matter further, population numbers in mixed concentrations of the two insects were sampled in 1949, by the usual procedure, approximately 2 weeks before the beetles had ceased feeding and again when 50 per cent. or more of each species had begun to aestivate. Four of the concentrations were just inside forests or plantations and four were at least 50 yd. from trees. The results are shown in Table 12. In the treeless sites the changes in the numbers of each species were variable. In area 3 a decrease was recorded for both. In area 9 the population density of C. *gemellata* increased, whereas that of C. *hyperici* did not change appreciably. The differences were negligible for both species in areas 10 and 11. In the timbered sites, the population changes shown by C. *hyperici* varied from a considerable decrease in area 4 to a substantial increase in area 8. The corresponding results for C. *gemellata* were very different. A marked decrease occurred in each area, the percentage fall ranging from 40 to 93.

As these large decreases could not be attributed to mortality*, it was concluded that most C. *gemellata* adults deserted the timbered sites before aestivation; whereas, except in area 4, any emigration by C. *hyperici* was compensated for by new arrivals. Subsequent observations indicated that a substantial proportion of the adults that moved out of timbered areas commonly aestivated near the tree margin in the leaf litter provided by the outer row of trees.

The tendency of the adults of both species to avoid occupying timbered areas persisted after the insects emerged from aestivation. Many of the beetles that had aestivated either along the boundaries of timbered areas or within them left their aestivation sites and migrated to treeless areas for oviposition. The majority of C. *gemellata* adults undoubtedly deserted the vicinity of timber, whereas the proportion of C. *hyperici* doing so varied considerably. Treeless areas, deficient in ground cover, in which the population was wiped out either during the winter or summer of 1949, were recolonized in 1950 by autumn migration from the margins of forests and plantations, e.g. areas 1*b* and 3*b* were recolonized by C. *gemellata* and areas 2*b*, 4*b*, and 5*b* by both species.

To illustrate the "preference" of C. *gemellata* for ovipositing in treeless areas, counts were made of the numbers of eggs laid within and outside the boundaries of two timbered sites in areas throughout which the density of *Hypericum* was similar. In one instance the C. *gemellata* adults had aestivated within the timbered area (a pine plantation) and, in the other, along the tree margin (of a eucalypt forest). Shortly before the counts the areas were searched carefully for aestivating adults. No living beetles were found in the clearings adjoining the timbered areas. The counts were made late in March, i.e. just before the peak of oviposition and before any eggs had hatched. Subsequent observations showed that the observed pattern of oviposition remained unchanged throughout the season.

In the first site 10 sample quadrats (2 by 2 lk.), 5 yd. apart, were counted for C. *gemellata* eggs along:

(*a*) A line 5 yd. outside the tree margin;

(*b*) A line 1 yd. outside the tree margin; and

(*c*) A line 5 yd. inside the tree margin.

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* Physical conditions were favourable and very few dead adults of either species were found. Possible predators and scavengers were numerous only in the forest sites 7 and 8. No predator that discriminates between the adults of C. *gemellata* and C. *hyperici* has been found in any habitat.

The mean egg densities and standard errors per square link were 2.53 ± 0.45, 7.80 ± 0.80, and 1.15 ± 0.69 respectively, indicating that most oviposition occurred just outside the tree margin.

In the second area, eight sample quadrats (2 by 2 lk.), 11 yd. apart, were counted for *C. gemellata* eggs along:

(*a*) A line 1.5 ch. within the eucalypt forest;
(*b*) A line 0.5 ch. within the eucalypt forest;
(*c*) A line 0.5 ch. outside the eucalypt forest;
(*d*) A line 1.5 ch. outside the eucalypt forest; and
(*e*) A line 2.5 ch. outside the eucalypt forest.

The mean egg densities and standard errors per sq. lk. were 0, 0.78 ± 0.45, 4.22 ± 0.64, 8.06 ± 1.39, and 5.13 ± 0.43 respectively. Most eggs were laid in the clearing roughly 1-2 ch. from the tree margin. Other observations in the area showed that a few *C. gemellata* adults migrated distances up to 4 ch. into the clearing shortly after aestivation ended. They moved very little after oviposition began.

Less detailed observations on *C. hyperici* in similar areas showed that some adults crawled at least 2 ch. into clearings from tree margins soon after emerging from aestivation. However, a large proportion of the beetles not infrequently remained close to where they had aestivated and oviposited on the wort plants beneath the trees.

A satisfactory explanation of the tendency of both insects to avoid dense timber cannot be given at present. The adults of *C. gemellata* and *C. hyperici* appeared to be both positively photokinetic and positively phototactic. Under some conditions the insects were more active in bright light than in shade and therefore accumulated in shaded positions (see also Wilson 1943). However, in the laboratory, at lower light intensities and temperatures than in bright sunlight, a definite tendency to move towards the incoming light was observed repeatedly. As the numbers of both species frequently decreased rapidly soon after they had entered dense timber, i.e. close to the tree margin, positive phototaxis may form the basis of the explanation. It is suspected that the basic difference between the two species, resulting in the greater tendency of *C. gemellata* to avoid remaining in timbered areas, is one of mobility. Under similar conditions, the adult of *C. gemellata* appeared to be a more mobile insect than the smaller *C. hyperici* adult.

VII. Fecundity of the Adult Females

Currie and Garthside (1932) gave the total egg production of the six longest-lived females collected during the course of their field work in England. These oviposited for 6½-9 months in the laboratory and produced from 1,839 to 3,752 eggs. Garthside, in an unpublished report, gave the mean egg production for 15 females, including these long-lived individuals, as 1,720 eggs. The mean for a subsequent batch of 36 females was 1,293 eggs. Wilson (1943) in his report on *Hypericum* insects in France, gave the mean egg production for females of *C. gemellata*, collected from the field, as 1,657 eggs. These workers did not describe adequately the conditions under with the observations were made. However, the figures are sufficient to show that both species are capable of producing very large numbers of eggs.

It is of interest to consider the actual fecundity of each species under field conditions in Australia. In 1949, estimations were made of the fecundity of each species (mean number of eggs per female) from counts made in 14 study areas containing 11 populations of each insect, suitable for the sampling of both eggs and reproducing adults. As the sex ratio was practically 50 : 50 in each species, the population density of females when oviposition began was taken as half the population density of adult beetles present at the time. For each study area, the total egg production of each species per sq. lk. was divided by the corresponding density of female beetles. The results are shown in Table 13.

TABLE 13

ESTIMATED MEAN FECUNDITIES OF *C. GEMELLATA* AND *C. HYPERICI* IN THREE TYPES OF STUDY AREA (1949)

Type of Study Area	Number of Study Areas		Estimated Mean Fecundity	
	1 *C. gemellata*	2 *C. hyperici*	1 *C. gemellata*	2 *C. hyperici*
Dense wort	6	5	527	252
Sparse wort	4	3	354	234
Timbered	1	3	78	268
Weighted mean fecundity for all populations and fiducial limits at the 5 per cent. level:			423 ± 143	251 ± 100

The estimated fecundities of *C. gemellata* ranged from 78 to 854 eggs, six results being between 300 and 400 eggs. The result for the only forest site was very much lower than the others. The means for dense wort and sparse wort study areas did not differ significantly. The fecundities of *C. hyperici* females ranged from 77 to 484 eggs per female. The means for the different types of study area were very similar. However, the result for one timbered area (77 eggs) was very much lower than the others. The fecundity of *C. gemellata* exceeded that of *C. hyperici* in all seven treeless sites in which paired comparisons were possible. The fecundities were almost equally low in the only timbered site in which a paired comparison could be made — 78 and 77 eggs for *C. gemellata* and *C. hyperici* respectively. Less extensive observations in 1950 yielded similar results. It was concluded that the average numbers of eggs produced per female of either species in the field were much lower than those recorded by overseas workers in the laboratory.

In 1950 a record was kept of the daily egg production of groups of adults (approximately 30 females and 30 males) kept in cages placed in the type sites at the Field Station. The cages were wire-gauze cylinders 10 in. long and 4 in. diameter. They were thrust between the mats of *Hypericum* and stood upright with the bases resting on the soil surface. Each afternoon a bunch of fresh *Hypericum* shoots was packed loosely into the basal half inch of each cage, providing foliage for food, oviposition, and cover. The cages were partially shaded by the dried flowering stems of the plants. Thus, natural conditions were imitated as closely as possible.

In the shade type site the mean daily temperature beneath the wort in the cages (where the insects lived) was, in general, approximately 2°F. lower than the mean recorded in a standard meteorological screen nearby (Fig. 1). The corresponding mean temperatures in cages kept in the other type sites were approximately 4°F. higher than those in the screen, i.e. 6°F. higher, on an average, than in the shade type site. Although the daily minima differed by only 2-3°F. in all cages, the daily maxima under the wort in those kept in the dense wort and sparse wort type sites were usually about 10°F. and 15°F. higher respectively than in the shade type site. Owing to the continuous presence of green, succulent feed around them in the cages, the insects probably experienced similar high humidities in all three sites.

TABLE 14

FECUNDITY OF FEMALES OF *C. GEMELLATA* AND *C. HYPERICI* KEPT IN CAGES IN THE TYPE SITES, 1950

	C. hyperici				*C. gemellata*			
Type Site	Cage 1*a*	Cage 2*a*	Cage 3*a*	Mean	Cage 1*b*	Cage 2*b*	Cage 3*b*	Mean
Dense wort	645	683	748	692	699	750	916	788
Sparse wort	558	667	700	642	731	623	535	630
Shade	567	462	500	510	1042	719	1081	947

The beetles used in the tests were collected from extensive areas immediately after emergence from aestivation, i.e. late February for *C. gemellata* and late April for *C. hyperici*. The fecundity of each cage group is shown in Table 14. *C. hyperici* laid most eggs in the dense wort type site and least in the shade type site, although the female mortality rate was slightly lower in the latter. The differences between sites were not great. On an average, more eggs were produced per female than in the field in 1949 and 1950. *C. gemellata* produced more eggs per female than *C. hyperici* in some cages. The mean fecundity of the former varied from being almost the same as that of *C. hyperici* in the sparse wort type site to much greater in the shade type site. The *C. gemellata* adults survived longest and laid most eggs in the coolest site. This result is of considerable interest in view of the marked tendency of *C. gemellata* to avoid remaining in densely timbered areas. As with *C. hyperici*, the number the eggs produced per female by *C. gemellata* in the cages appeared to be substantially higher, on an average, than in the field.

In these tests approximately 30 per cent. of the *C. gemellata* females continued to oviposit nightly for over 8 months, and 35 per cent. of the *C. hyperici* females continued to do so for approximately 7 months. In the field, both in 1949 and 1950, very few adults of either species survived for as long as 2½ months after oviposition began. The comparatively early deaths of most individuals appeared to be due mainly to extrinsic mortality factors (Section IX).

VIII. Fertility of the Eggs

The procedure adopted for the estimation of infertility was to record the percentage of eggs showing no signs of development and failing to hatch in random samples (generally 200-250 eggs), collected at intervals of 4-5 weeks throughout the autumn and winter, and kept in the type sites in the usual way.

This method could sometimes have over-estimated the proportion of infertile eggs because a few individuals in some samples were attacked by fungi. It was not always possible to ascertain if they were non-viable or killed by the fungi. The majority of infertile eggs, whatever the prevailing conditions, collapsed within 3 weeks of laying. The remainder were easily recognized by the appearance of the yolk a few weeks after oviposition. The fact that most infertile eggs collapsed, shrivelled, and disappeared from the *Hypericum* foliage in a comparatively short time meant that there was little accumulation of infertile eggs on the weed. Thus an increase in the proportion of infertile eggs with time was due principally to an increase in the proportion laid.

Table 15

FREQUENCY DISTRIBUTION OF PERCENTAGE INFERTILITY IN SAMPLES OF EGGS COLLECTED IN 1950

Mid values of classes (%)	1.75	5.35	8.95	12.55	16.15	19.75
Frequency	16	32	20	14	7	3

Table 15 shows the percentages of eggs that failed to hatch from samples collected from 19 study areas between April and August 1950. The mean infertility of the 92 samples was 7.9 per cent. To obtain some idea of the percentage infertility in eggs of each species, the egg batches collected during each sampling were considered in detail. The results are summarized in Table 16, in which the mean percentage of *C. gemellata* eggs, based on the fertile eggs in each batch, is shown for each sampling.

Experience from handling some thousands of eggs in various observational trials and tests at the Field Station during 1949 and 1950 gave the impression that the mean percentage infertility in eggs of each species increased from approximately 5 per cent. soon after laying began to approximately 10-15 per cent. late in the oviposition period. The figures for samplings IV, V, and VI appear to be in accordance with this suggestion as far as *C. hyperici* is concerned. Infertility in *C. gemellata* may also have increased as the season advanced. For example, any increase between samplings II and III would tend to be concealed by the presence of a higher proportion of *C. hyperici* eggs, which would be approximately 95 per cent. fertile at this time of the year, according to general observation. If, in fact, the mean infertility of the *C. hyperici* eggs was 5 per cent. for samplings II and III, the means for *C. gemellata* would have been approximately 11 per cent. and 13 per cent. respectively.

If the percentage infertility of *C. gemellata* eggs was considerably higher than that of *C. hyperici* eggs at this time, one would expect a positive correlation between percentage infertility and the percentage of *C. gemellata* in the fertile eggs for samplings II and III, both of which contained egg lots in which the proportion of this species ranged from high to low values. The results for the two samplings were pooled and a positive correlation was found ($r = 0.359$: significant at the 5 per cent. level).

TABLE 16

MEAN PERCENTAGE INFERTILITY IN SAMPLES OF EGGS COLLECTED DURING 1950 IN RELATION TO THE MEAN PERCENTAGE OF *C. GEMELLATA*

Sampling No. —	I	II	III	IV	V	VI
Sampling Period:	Early to Mid April	Late April to Early May	Mid to Late May	Mid to Late June	Mid to Late July	Late August
Mean percentage infertility	7.7	9.3	7.8	6.7	6.2	14.5
Range in percentage infertility	2.0-17.2	0.9-17.6	3.3-16.7	2.8-19.2	0.0-12.2	6.4-20.8
Mean percentage *C. gemellata*	100	71	34	17	6	8
Range in percentage *C. gemellata*	—	12-100	1-86	0-42	0-22	2-13
Number of samples	18	19	15	18	17	5*

* The small number of samples was due to the fact that hatching was almost complete and egg numbers were low almost everywhere.

To form some idea of the percentage infertility in each species for the whole of the eggs produced during the year, the seasonal egg distributions require consideration. Egg numbers of *C. gemellata* reached their maxima in April or early May. The mean infertility for egg batches collected when the maxima occurred was 8.58 per cent. and the range 2-17.2 per cent. The corresponding mean percentage of *C. gemellata* eggs was 94 per cent. If nearly all of the few *C. hyperici* eggs present at the time were fertile, the percentage infertility of the *C. gemellata* eggs would have been approximately 9 per cent. The eggs present in each study area when the maximum occurred formed 45 per cent. or more of the total production. Infertility might have been lower in the eggs laid prior to those contributing to the maxima, and higher in those laid after; but, as the differences would tend to cancel out, it is probable that the overall mean infertility was close to 9 per cent. Similarly, the overall mean infertility in eggs of *C. hyperici* was probably about 6 per cent.

The possibility that the percentage infertilities of eggs of *C. gemellata* and *C. hyperici* were higher in timbered areas than in clearings was examined by comparing adjacent pairs of timbered and treeless sites. The results for four such pairs are shown in Table 17. They provide no evidence to suggest that the overall infertility in eggs of either species was higher in timbered areas.

Similarly, the results for more widely separated timbered and treeless areas showed no consistent differences for either *C. gemellata* or *C. hyperici.*

IX. Causes of Mortality

(*a*) *Temperature*

(i) *Frost.*—Field experiments showed that the survival rates of eggs of *C. gemellata* and *C. hyperici* were not affected appreciably by severe frosts ("grass" temperatures down to 10°F.) even when they occurred repeatedly. However, the larvae and reproducing adults of both species were less resistant. The most susceptible stage appeared to be the first-instar larva, either because of its habit of remaining on the procumbent shoots of the weed or because of lower physiological resistance.

Table 17

Percentage infertility of eggs collected in timbered and treeless areas, and estimated percentage of *C. gemellata* eggs present in the samples

	Sampling No.									
	I		II		III		IV		V	
Site	% Infertility	% *C. gemellata*	% Infertility	% *C. gemellata*	% Infertility	% *C. gemellata*	% Infertility	% *C. gemellata*	% Infertility	% *C. gemellata*
Pine plantation (*a*)										
(i) In trees	2	100	4	61	4	7	8	3	8	0
(ii) In adjacent clearing	2	100	17	96	7	40	14	23	11	3
Pine plantation (*b*)										
(i) In trees	5	100	8	52	5	13	5	14	10	6
(ii) In adjacent clearing	6	100	12	85	10	13	4	12	5	2
Eucalypt forest (*a*)										
(i) In trees	8	100	10	96	9	84	—	—	—	—
(ii) In adjacent clearing	5	100	16	82	8	23	6	25	4	6
Eucalypt forest (*b*)										
(i) In trees	—	—	—	—	5	1	8	0	0	0
(ii) In adjacent clearing	12	100	9	60	7	26	19	10	0	0

In a preliminary test made in 1949, shallow dishes containing 8-30 newly hatched larvae, occupying their usual positions on *Hypericum* shoots, were left on an area of bare ground on each of the 12 frosty nights occurring between July 30 and August 18. Corresponding control batches were kept beneath the mats of *Hypericum* in an adjacent stand of the weed. Throughout the study period the test batches were placed beside the control lots during the day and on cloudy nights. The shoots of *Hypericum* were replaced daily; and additional larvae were included in an attempt to imitate the almost daily hatching that occurred in the field. Five severe frosts occurred during the period. The associated minimum temperatures recorded by thermometers lying beside the test dishes ranged from 14 to 20°F. The corresponding minimum temperatures for the control batches ranged from 25 to 33°F. A variable proportion of the test larvae died during or immediately after each severe frost. The total mortality at the end of the period ranged from 95 to 100 per cent. for both *C. gemellata* and *C. hyperici.* No deaths occurred in the controls. Thus it appeared that the repeated occurrence of temperatures of 20°F. or lower caused very high mortalities to the newly hatched larvae of both species.

Similar tests were made in the laboratory using a refrigerator. Small batches of first-star larvae, several days old and adequately fed, were exposed nightly for 10 hours to temperatures of 30, 25, and 20°F. and relative humidities close to 100 per cent. During the day the dishes containing test larvae were placed beside those containing control batches, which were kept continuously at room temperatures. Tests were also made for very short periods at 17°F., using first-instar larvae of *C. gemellata* and all four stages of *C. hyperici.* Before exposing larvae to 17°F. they were first subjected to 35°F. and then to progressively lower temperatures down to 25°F. for a total period of 6-10 hours to imitate the steady fall to the minimum that occurred in the field.

The results are summarized in Table 18. For larvae exposed to temperatures of 20-30°F., and the corresponding controls, survival was computed at the end of the larval feeding period. For larvae exposed to 17°F. the percentage survival was determined three days after the test. The variability shown by the results is attributed partly to differences in individual susceptibility and partly to slight differences in the actual conditions experienced by individual larvae. At 30°F. the larvae of *C. gemellata* survived long periods of nightly exposures without appreciable mortality. The corresponding results for *C. hyperici* suggest that low mortalities were caused by the treatment. Long test periods at 25°F. resulted in high mortalities to both species. Shorter test periods at 20°F. caused similar or higher mortalities. Half an hour at 17°F. was sufficient to kill most first-instar *C. gemellata* larvae. First-instar larvae of *C. hyperici* showed higher survivals after half an hour at 17°F. A comparison of the results for all instars of this species suggests that the first instar is the most resistant stage, and that resistance to low temperatures decreases with age.

As a whole the results of these tests suggest that larval mortality could occur in the field either as the immediate result of a frost temperature less than 20°F. or as the ultimate result of repeated frosts with slightly higher minimum temperatures. The fact that the first-instar larvae of *C. hyperici* were, if anything, more resistant to low temperatures than older larvae indicates that the relatively high mortality of the former in the field was due

TABLE 18

EFFECT OF LOW TEMPERATURES ON THE SURVIVAL OF LARVAE OF *C. GEMELLATA* AND *C. HYPERICI* (REFRIGERATOR TESTS)

Date Started	Species and Instar	Number of Batches	Treatment	Percentage Survival, Batches Pooled if More than 1	Days Lived Before Death, Mean and Range	Percentage Survival in Control	Extreme Range of Temperatures Affecting Controls
30°F.							
26-4	*C. gemellata* 1st	1	60 nights	100	—(–)	100	35–68°F.
2-7	*C. gemellata* 1st	1	50 nights	86	23(–)	83	30–55°F.
15-9	*C. gemellata* 1st	1	36 nights	100	—(–)	100	43–72°F.
2-7	*C. hyperici* 1st	1	50 nights	80	36(22–49)	90	30–55°F.
15-9	*C. hyperici* 1st	2	36 nights	89	30(28–32)	100	43–72°F.
25°F.							
11-8	*C. gemellata* 1st	1	54 nights	11	19(4–46)	92	36–70°F.
4-9	*C. gemellata* 1st	2	46 nights	44	27(7–46)	100	36–72°F.
15-9	*C. gemellata* 1st	1	34 nights	0	13(6–34)	100	43–72°F.
4-7	*C. hyperici* 1st	2	36 nights	3	26(8–35)	88	30–55°F.
11-8	*C. hyperici* 1st	2	50 nights	0	24(10–52)	96	36–70°F.
20°F.							
26-4	*C. gemellata* 1st	1	12 nights	0	7(3–12)	100	35–68°F.
1-5	*C. gemellata* 1st	3	12 nights	7	7(1–25)	91	33–65°F.
11-5	*C. gemellata* 1st	3	9 nights	5	5(2–7)	89	30–63°F.
2-7	*C. hyperici* 1st	4	10 nights	3	4(1–9)	88	30–55°F.
17°F. after "conditioning"							
5-9	*C. gemellata* 1st	2	0.5 hr.	15	—	100	38–58°F.
28-8	*C. hyperici* 1st.	2	1.5 hr.	21	—	100	38–61°F.
25-9	*C. hyperici* 1st.	1	0.75 hr.	0	—	100	55–67°F.
4-9	*C. hyperici* 1st	2	0.5 hr.	53	—	100	36–61°F.
5-9	*C. hyperici* 1st	2	0.5 hr.	25	—	100	38–58°F.
25-9	*C. hyperici* 1st.	2	0.5 hr.	37	—	100	55–67°F.
4-9	*C. hyperici* 2nd	2	0.5 hr.	25	—	100	36–61°F.
25-9	*C. hyperici* 2nd	1	0.5 hr.	8	—	100	55–67°F.
25-9	*C. hyperici* 2nd	1	0.75 hr.	0	—	100	55–67°F.
28-8	*C. hyperici* 3rd	2	1.5 hr.	0	—	100	38–61°F.
4-9	*C. hyperici* 3rd	2	0.5 hr.	10	—	100	36–61°F.
25-9	*C. hyperici* 3rd	2	0.5 hr.	0	—	100	55–67°F.
28-8	*C. hyperici* 4th	2	1.5 hr.	0	—	100	38–61°F.
20-9	*C. hyperici* 4th	2	1.5 hr.	0	—	100	49–58°F.
21-9	*C. hyperici* 4th	2	0.5 hr.	0	—	100	45–61°F.
25-9	*C. hyperici* 4th	2	0.5 hr.	0	—	100	55–67°F.

to their habit of remaining continuously on the plants. The older larvae spent part of the night beneath the *Hypericum* mats in places where the temperatures ranged from 2 to 5°F. higher than at the surfaces of the procumbent growth, depending on the amount of cover present. It is possible that the habit of clustering during resting periods (Section IV) also aided their survival. This interpretation of the relatively high mortality suffered by first-instar larvae is assumed to apply also to *C. gemellata.*

To estimate the frequency of "killing" frosts in the study areas, thermometers were laid on the mats of *Hypericum* and a record obtained of the minimum temperatures occurring on 15 frosty nights in each. The "site" temperatures so determined in each area were plotted against the corresponding minima recorded in a standard screen at the Field Station. In each case a well-defined linear relationship was apparent. A regression equation was therefore computed for each study area from which it was possible to estimate the site temperature corresponding to any screen minimum temperature when frost occurred. (When the site temperatures for different areas were almost identical the re-

TABLE 19

RELATIONSHIP BETWEEN SITE AND SCREEN TEMPERATURES FOR THE STUDY AREAS; ESTIMATED MINIMUM SITE TEMPERATURES IN 1949; AND ESTIMATED NUMBERS OF FROST DAYS WITH SITE TEMPERATURES < 20 AND < 25°F. (GIVEN ONLY WHEN THE SPECIES WAS PRESENT)

Study Area	Regression Equation x = Screen Temperature y = Estimated Site Temperature	Estimated Minimum Site Temperature, 1949 (°F.)	Estimated No. of Frost Days, Site Temperature < 20°F.		Estimated No. of Frost Days, Site Temperature < 25°F.	
			For *C. gemellata* Larvae	For *C. hyperici* Larvae	For *C. gemellata* Larvae	For *C. hyperici* Larvae
Dense wort						
1*a*	$y = 0.9846x - 6.3457$	14	18	10	68	40
2*a*	$y = 0.7059x + 0.5113$	15	31	22	83	57
3*a*	$y = 1.3077x - 12.2118$	15	8	7	41	24
4*a*	$y = 0.9615x - 4.3038$	16	15	10	62	37
5*a*	$y = 1.3077x - 12.2118$	15	8	—	41	—
6*a*	$y = 0.9615x - 4.3038$	16	15	10	62	37
7*a*	$y = 0.9615x - 4.3038$	16	15	10	62	37
Sparse wort						
1*b*	$y = 1.1538x - 15.5306$	9	60	37	85	59
2*b*	$y = 1.2297x - 10.7366$	15	8	7	42	24
3*b*	$y = 0.7346x + 4.7828$	20	0	—	31	—
4*b*	$y = 1.5000x - 22.2500$	9	31	20	68	40
5*b*	$y = 1.6667x - 25.8010$	9	31	20	60	37
Timbered						
1*c*	$y = 0.8750x + 7.5937$	26	0	0	0	0
2*c*	$y = 0.6939x + 13.7115$	28	0	0	0	0
3*c*	$y = 1.0308x + 1.2743$	23	—	0	—	4
4*c*	$y = 1.2000x - 3.7667$	21	0	0	6	4
5*c*	$y = 1.8000x - 22.9600$	15	—	1	—	11

sults were pooled and a single relationship computed.) From the relationships and the 1949 screen temperature records, estimates were made of the numbers of frost nights when the site temperatures were less than 20 and 25°F., and larvae of *C. gemellata* and *C. hyperici,* including the first instar, were present. They are shown in Table 19 together with the regression equations and the estimated minimum site temperature occurring in each study area in 1949.

The results for the treeless study areas show that severe frosts, potentially capable of killing larvae of *C. gemellata* and *C. hyperici,* occurred repeatedly (except possibly in area 3*b*). Although fewer severe frosts were recorded for *C. hyperici* than for *C. gemellata,* most occurred during the peak hatching period. As dead and dying individuals were found in considerable numbers whenever these areas were visited immediately after severe frosts, it was concluded that the total losses suffered by each species during the winter must have been high in most areas. In area 1*b* the only survivors in a mixed larval population of the two species were prepupae of *C. gemellata* in the soil. The few survivors in the mixed population in area 4*b* were *C. hyperici* individuals, the majority of which were in the egg stage when the most severe frosts occurred. In the timbered study areas, the minimum temperatures occurring when larvae of *C. hyperici* and *C. gemellata* were present were too high to have caused substantial losses. This was confirmed by check experiments made in the shade type site.

Laboratory and field observations, similar to those described for larvae, were made on the reproducing adults of both species. The laboratory tests indicated that their susceptibility to low temperatures was similar to that of first-instar larvae. However, most *C. gemellata* adults died each year before the period of severe frosts began, showing that other factors were responsible. Many of the reproducing adults of *C. hyperici* died during the coldest months, and some might have been killed by frosts in treeless areas. It is suspected that the proportions destroyed in this way were not very high. Like the older larvae, the adults did not expose themselves to the same extent as first-instar larvae after oviposition commenced.

(ii) *High Temperatures.*—During the late springs of 1948, 1949, and 1950, large numbers of dead and dying adults of *C. gemellata* and *C. hyperici* were found in some treeless areas. These high mortalities occurred after the formation of "feeding fronts."* During the day many of the beetles remained on the erect stems of plants defoliated the previous night and were thus exposed to direct solar radiation. In this, they differed from individuals too low in density to defoliate the host plant appreciably. They, too, characteristically remained on the erect stems, but frequently sought the shade of the foliage and flowers during the hottest periods of the day (see also Wilson 1943).

The areas in which high mortalities occurred were all relatively hot places in which the "sun" temperatures (as measured by ordinary mercury-in-glass thermometers) not infrequently reached 104°F. (40°C.) 18 in. above ground level and over 140°F. (60°C.) at the surface of the debris on the ground. Some of the most spectacular mortalities occurred during periods of high humidity following heavy rains. In all cases, however, the dead and dying insects exhibited the same appearance. Most were intact and none showed any signs of disease. Many had obviously vomited the crop contents before death, and some had died with the elytra raised and wings extended as for flight. It appeared that the insects had been killed by high temperatures, aided sometimes by high humidities (cf. Wilson 1943).

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* Feeding fronts, which are dense concentrations of the adults, are formed after the insects have defoliated part of a stand of *Hypericum.* The individuals of each species accumulate on previously unattacked plants surrounding the zone of defoliation and advance *en masse,* eating their way slowly through the stand (Clark and Clark 1952).

Laboratory tests showed that the adults of both species were killed readily by exposure to high temperatures in sunlight. In one test over 50 per cent. of each species (60 individuals used) reached a state of heat stupor after being exposed for 40 minutes in sunlight to temperatures rising steadily from 86°F. (30°C.) to 108°F. (42.2°C.). All were inactive after 60 minutes, by which time the temperature had reached 111°F. (43.9°C.). None recovered after removal to a cooler place (70°F.). There was no mortality in corresponding batches kept at 60-70°F. in the shade. Before becoming inactive most beetles exhibited abnormally great activity, vomiting, and wing spreading. Some attempted to fly at temperatures between 86°F. and 97°F. (Section IV). A second test gave a similar result; and showed also that, at relative humidities close to 100 per cent., distress symptoms and stupor began at sun temperatures 6-8°F. lower than at room humidities ($<$ 70 per cent.). This provides a possible explanation of the crashes observed in the field a few days after heavy rains.

High temperatures were probably also responsible for a large part of the very high mortality that occurred during the aestivation period. In Section VI it was shown that survival during this interval occurred only where the amount of protective plant cover was relatively high. Associated with the site differences in plant cover were marked differences in the temperatures occurring in the places occupied by the beetles beneath the plant debris. In sites 4-6 (Table 11) the daily maximum temperatures rarely exceeded 86°F. In sites 1-3, where some individuals of each species also survived, the daily temperatures beneath the debris sometimes exceeded 104°F. for an hour or so. In sites 11-13, in which no survival occurred, the daily temperatures beneath the debris frequently exceeded 113°F. (45°C.) for periods of 1-3 hours in many places. It appears that all of the mortality occurring in the last-mentioned sites could have been due to overheating. In the other sites, desiccation was probably involved to a varying extent. Site 4, where the mortality of both species appeared to be lowest, provided the most humid conditions. In this area only, much of the soil surface remained damp throughout the summer.

(*b*) *Moisture*

(i) *Desiccation*.—Apart from its probable effect on adult survival during the aestivation period, desiccation could rarely have influenced population numbers significantly. The only other stage affected appreciably during the study period was the egg. The experiments described in Section V (Table 7) showed that mortality occurred in the eggs of both species as a result of water loss. The mean percentage mortalities of the *C. gemellata* eggs in experiments 1-3, attributable to desiccation, were 25, 10, and 30 per cent. respectively. These losses are small considering the severity of the desiccation. The *C. hyperici* eggs were much more susceptible, only 4.5 per cent. of fertile eggs surviving in experiment 3.

During the late autumns and winters of 1949 and 1950, the proportion of collapsed fertile eggs in the population samples never exceeded 2 per cent. for *C. hyperici,* showing that few individuals could have been destroyed by desiccation in spite of their susceptibility. In all study areas, the losses suffered by *C. gemellata* throughout its entire oviposition period were similar. Elsewhere, substantial losses due to desiccation occurred only when the adults of this species emerged from aestivation much earlier than usual. In such rare cases, oviposition began in February under conditions sufficiently dry to cause the *Hypericum* foliage to wilt during the day.

As it was possible that larval mortality could occur as the result of water losses suffered during the egg stage, the survival rates of individuals hatching from the desiccated and non-desiccated eggs used in experiment 3 (Table 7) were determined at the end of the larval feeding period. All four *C. hyperici* larvae from desiccated eggs survived. The mean survivals for *C. gemellata* individuals from desiccated and non-desiccated eggs were 85 and 84 per cent. respectively. Thus the subsequent survival was not affected appreciably by the moisture conditions experienced during the egg stage.

(ii) *Soil Moisture.*—During the relatively dry winter of 1949, mortality attributable definitely to soil moisture conditions was observed only in the timbered areas, 2*c* and 4*c*, in which the soil beneath the thick mat of pine needles remained wet almost continuously. Population sampling showed decreases of approximately 61 and 64 per cent. respectively in the soil populations of *C. gemellata* before many individuals had reached the pupal stage. The losses appeared to be due either to flooding of the pupal cells or to saprophytic fungi, which were found growing on dead and apparently dying individuals.

Over 12 in. of rain fell during the early spring and the pupal cells in all study areas were flooded repeatedly. Dead prepupae and pupae of both species were found during October in both treeless and timbered areas. Because of its earlier emergence from the soil (Section IV), *C. gemellata* escaped the wettest conditions and suffered comparatively small losses in all areas. *C. hyperici* experienced the full impact of the wet conditions and suffered heavy prepupal losses in timbered areas and in some treeless areas. Of the eight treeless study areas in which the spring prepupal and pupal losses were estimated, four were well-drained sites with light soils (2*a*, 3*a*, 2*b*, and 5*b*) and four were situated on heavier soils in slight depressions (1*a*, 4*a*, 6*a*, and 7*a*). The estimated mean spring mortality of the soil population for the well-drained areas was 30 per cent. for *C. gemellata* and 14 per cent. for *C. hyperici*. The corresponding means for the low-lying sites were 21 per cent. and 67 per cent.

for *C. gemellata* and *C. hyperici* respectively. The difference was significant for *C. hyperici* only. The following year almost 11 in. of rain fell in September and October, and *C. hyperici* again suffered heavy losses in some places, whereas *C. gemellata* escaped lightly.

During 1950 laboratory tests were made to ascertain if the prepupae of each species were readily drowned by immersion in water. In all tests the majority of individuals survived several days continuous immersion. However, all or nearly all prepupae died soon after. Weighing experiments on lots of 50 prepupae of each species before and after immersion for varying periods showed that they absorbed water in some way. All were noticeably distended after several days immersion; whereas the corresponding controls, kept at 100 per cent. relative humidity, lost a small amount of water. The average daily increase in body weight for immersed larvae ranged from 4 to 10 per cent. approximately. Similarly swollen individuals were not uncommon in the wetter study areas used in 1949 and 1950. Thus it seems likely that some at least of the deaths recorded were due to absorption of water when the pupal cells were flooded.

(*c*) *Dislodgment of Eggs from the Plant*

Some eggs of both species were dislodged from the *Hypericum* foliage before hatching. Most of these eggs were attacked by common saprophytic fungi. Laboratory examinations of attacked eggs suggested that they continued to develop until the organisms penetrated the chorion and continued growth on the contents. Few individuals survived contamination.

This loss of eggs from the plants required investigation, not only as a source of mortality, but also in connection with estimation of the total egg production of each species. Dislodgment *during the period that oviposition was in progress* would cause underestimation of the total production. To illustrate the point, consider the third method employed for estimating total egg numbers. This allowed only for:

(i) Eggs that remained on the plants until hatching;

(ii) Eggs that fell from the plants after a count, but completed their development before the next count was made, i.e. hatched during the interval when dislodgment occurred.

For each fallen egg that did not hatch during the interval when dislodgment occurred a new egg was missed. In effect, the new egg was counted as the dislodged egg, which should have been on the plant when the second population count was made.

Field observations showed that the proportion of *C. gemellata* eggs that fell from the plants during the autumn, i.e. when eggs of the species were most numerous and development most rapid, was very low. It was not until after the rate of egg development had decreased greatly that substantial losses were observed. They were undoubtedly greatest in timbered areas, in which development took longer than elsewhere (Sections IV and V). However, the losses did not occur until oviposition had either ceased or declined to a very low rate in all study areas. It was concluded that, although the mortality resulting from dislodgment was considerable in treeless areas and fairly high in timbered areas, the losses from the plants were negligible from the viewpoint of population assessment.

Similar preliminary observations made on *C. hyperici* eggs in 1948 suggested that the mortality due to dislodgment was considerably higher than that suffered by *C. gemellata,* and worthy of further study as a cause of error in population estimations. Counts of the fallen eggs made in the study areas used in 1949 showed an almost continuous loss from the plants in all habitats, beginning late in May. In June and July it appeared that 5-10 per cent. of the eggs present were dislodged each month, irrespective of habitat and population density. In August, when laying had ceased, the proportional losses were higher. In treeless areas, the actual numbers dislodged then were comparatively low because many eggs had already hatched. In timbered areas, where the peak of hatching occurred some weeks later, the losses from the plants from late July to mid September represented roughly 25-50 per cent. of the total production. The subsequent mortality, due principally to fungal attack, must have been nearly as high. It is estimated that the mortality suffered by *C. hyperici* in this way was about 1.5 times that of *C. gemellata* in each of the principal types of habitat.

To obtain more precise figures on egg dislodgment for *C. hyperici,* an observational trial was carried out in 1950 in a treeless area protected from frost and bearing a tall, dense stand of *Hypericum.* Four contiguous plots were used, each 0.25 sq. yd. in area. First, the distribution of eggs was recorded on plant maps, after which pieces of cloth were fitted carefully under each plant. At intervals similar to those between counts made in the study areas, the presence of new eggs was recorded on the maps and the hatched eggs, dislodged eggs, and first-instar larvae were removed and counted. From the map records and counts a checked estimate was made of the total number of eggs produced; and the number of fallen eggs that failed to complete development to eclosion during the interval when dislodgment occurred was determined precisely. The results may be summarized as follows:

(i) The proportion of eggs dislodged was independent of the population density.

(ii) The mean daily rate of fall of eggs that did not hatch during the interval when dislodgment occurred was approximately 0.3 per cent. for both June and July.

(iii) The total fallen eggs for June and July that failed to hatch during the interval when dislodgment occurred, formed approximately 10 per cent. of the total production; suggesting that this proportion was missed by the methods used for assessing total egg numbers in the study areas.

The only possible causes of egg dislodgment that account satisfactorily for its apparent independence from population density, sustained regularity under variable rainfall conditions, and increase late in the season, are:

(i) Growth of the end leaves in the *Hypericum* mats and consequent breaking of the dried secretion that attaches the eggs.

(ii) Shedding of leaves by the plants.

A high percentage of the eggs of *C. hyperici* were laid in the tips of the *Hypericum* shoots, i.e. on small, young leaves, which grew slowly throughout the winter until August when the rate increased with the onset of warmer conditions. As the winter advanced the *Hypericum* mats shed a gradually increasing number of leaves. After August the rate of leaf fall accelerated more rapidly until October when the mats withered and died. In treeless areas, most *C. hyperici* eggs hatched before marked increases occurred in the growth rate and fall of the leaves; but, in many timbered areas, the peak of hatching followed the early spring accelerations in these processes.

The egg dislodgment suffered by *C. gemellata* is considered to have been less than that of *C. hyperici* because:

(i) A large proportion of individuals completed development in a comparatively short time;

(ii) Relatively more eggs were laid on leaves that had practically completed growth; and

(iii) The rate of leaf fall was very low when eggs of *C. gemellata* were numerous.

For both species, leaf growth appeared to cause much higher losses than leaf fall.

(*d*) *Predation*

(i) *By Birds*.—Preliminary observations made in 1948 suggested that only seven species of insectivorous birds were likely to feed to any extent on the larvae of *C. gemellata* and *C. hyperici*. They are listed in Table 20. Small numbers of each species were shot the following year in areas containing substantial larval populations of the beetles. The relevant information provided by examinations of the gizzard contents is summarized in the table. Apparently the birds did not eat the small first- and second-instar larvae as only older individuals were present. Only three of the 27 birds shot in the areas in which the *Hypericum* mats were not substantially defoliated contained *Chrysomela* larvae. In each the bulk of the food material was formed by other insects and spiders, varying greatly in size. A very different result was shown by birds shot where the *Hypericum* had been defoliated completely by *Chrysomela* larvae. In such areas, the larvae had destroyed much of their protective cover, and many wandered about during the day in search of food. As indicated, most of the birds contained larvae of either *C. gemellata* or *C. hyperici*. Some contained practically no other prey. After further observations on their feeding habits and numbers, it was concluded that birds had little effect on larval populations of either species of *Chrysomela* where the host plant retained most of its foliage. Where the foliage had been consumed, most of the larvae taken by birds would have died of starvation (see later).

Each year the adults of *C. gemellata* were attacked by birds (Table 21) after they had emerged from aestivation in numbers greatly depleted by summer mortality due to other factors. Examinations of the gizzard contents showed that some birds, notably *Corcorax, Colluricincla,* and *Strepera,* continued to feed on *C. gemellata* adults after they had begun to conceal themselves beneath the *Hypericum* mats. Such birds found the reproducing adults even in areas in which the mats of *Hypericum* had not been defoliated appreciably by larval feeding. The same birds did not feed much on the more numerous *C. gemellata* larvae, present at the time, except where the weed had been defoliated. *Corcorax* was never observed to feed on *Chrysomela* larvae. Possibly the adult beetles were found much more easily because of their bright coloration.

TABLE 20

BIRDS FEEDING ON THE LARVAE OF *C. GEMELLATA* AND *C. HYPERICI*, 1949

Species	No. Shot in Undefoliated *Hypericum* Stands	No. Containing Chrysomelid Larvae	No. Shot in Defoliated *Hypericum* Stands	No. Containing Chrysomelid Larvae	Maximum No. Larvae in any Bird
Blue wren (*Malurus cyaneus*)	5	0	3	2	17
Yellow robin (*Eopsaltria australis*)	5	0	2	2	6
Yellow-tailed thornbill (*Acanthiza chrysorrhoa*)	2	0	1	1	20
Grey shrike thrush (*Colluricincla harmonica*)	5	1	4	3	79
Scrub wren (*Sericornis frontalis*)	3	0	2	1	3
Scarlet robin (*Petroica multicolor*)	2	0	1	1	5
Grey currawong (*Strepera versicolor*)	5	2	8	7	175
Totals	27	3	21	17	

The autumn bird attack coincided with a rapid dwindling of the numbers of *C. gemellata* adults, which began in March, soon after emergence from aestivation, and continued during April after oviposition had commenced. The available evidence suggests that predation by birds was the principal extrinsic cause of mortality both before and after the *C. gemellata* adults began to conceal themselves beneath the *Hypericum*.

When the *C. hyperici* adults appeared on the plants after aestivation they were also attacked by birds. The destruction continued after the insects had begun to hide beneath the *Hypericum* mats. Some birds shot in July contained *C. hyperici* adults. In the writer's opinion they probably destroyed as many reproducing adults of this species as did frosts.

TABLE 21

BIRDS FEEDING ON ADULT CHRYSOMELIDS DURING 1949 (SHOT IN AREAS CONTAINING ADULT BEETLE POPULATIONS OF HIGH AND LOW DENSITY)

Species	No. Shot in Defoliated Stands of *Hypericum*	No. Containing Adult Beetles	No. Shot in Relatively Undamaged Stands of *Hypericum*	No. Containing Adult Beetles	Maximum No. of Adult Beetles in Gizzards
Blue wren* (*Malurus cyaneus*)	8	5	8	4	3
Yellow robin* (*Eopsaltria australis*)	3	2	1	1	2
Yellow-tailed thornbill* (*Acanthiza chrysorrhoa*)	2	1	2	0	2
Buff-tailed thornbill* (*A. reguloides*)	–	–	2	1	1
Grey shrike thrush* (*Colluricincla harmonica*)	4	4	5	5	30
Scrub wren* (*Sericornis frontalis*)	3	1	2	2	2
Eastern shrike tit (*Falcunculus frontatus*)	1	1	–	–	2
Silver eye (*Zosterops halmaturina*)	3	2	–	–	4
Olive-backed oriole (*Oriolus sagittatus*)	–	–	1	1	62
Pipit (*Anthus australis*)	1	1	1	1	1
Dusky wood swallow (*Artamus cyanopterus*)	1	1	1	1	25
Crimson rosella (*Platycercus elegans*)	2	1	1	0	3
Rufous whistler (*Pachycephala rufiventris*)	6	6	–	–	5
Black-faced cuckoo shrike (*Coracina novae-hollandiae*)	4	4	1	1	41
Yellow-faced honeyeater (*Meliphaga chrysops*)	5	5	–	–	5
Grey currawong* (*Strepera versicolor*)	2	2	7	7	84
Spotted quail thrush* (*Cinclosoma punctatum*)	–	–	2	2	4
White-winged chough* (*Corcorax melanorhamphus*)	3	3	8	7	76
Totals	48	39	42	33	

* Birds feeding on adult chrysomelids during the autumn and winter as well as during the spring.

Early in the spring, bird numbers increased greatly with the arrival of nomadic and migrant species, many of which attacked the new generation of adult beetles (Table 21). The winter residents and newcomers began to feed

TABLE 22

LARVAL NUMBERS OF THE CHRYSOMELIDS IN EUCALYPT FOREST AND OTHER AREAS

C. gemellata

Stage	Counts (numbers per 9 quadrats, each 3 to 3 lk.)											
	I (Late April)			II (Late June)			III (Mid July)			IV (Late August)		
	1*c*	2*c*	*x*	1*c*	2*c*	*x*	1*c*	2*c*	*x*	1*c*	2*c*	*x*
Eggs	51(+1)*	48(+7)*	390(+87)*	5	14	88	1	20	89	1	5	14
Feeding larvae	36	29	33	25	9	225	12	12	102	0	8	53
Resting larvae and pupae	0	0	0	0	23	133	0	14	142	0	9	231
Total	88	84	510	30	46	446	13	46	333	1	22	298

C. hyperici

Stage	Counts (numbers per 9 quadrats, each 3 by 3 lk.)							
	I (Late August)				II (Late September)			
	1*c*	3*c*	*x*	1*a*	1*c*	3*c*	*x*	1*a*
Eggs	5	6	60	4	0	2	8	0
Feeding larvae	28	26	76	54	5	10	84	0
Resting larvae and pupae	0	0	0	0	0	0	37	40
Total	33	32	136	58	5	12	129	40

* The figure in brackets is the estimated number of eggs laid after this date. Thus the totals given represent the total numbers of individuals produced between late April and late August.

heavily on the young beetles a few weeks after their emergence from the soil. Although the adults of *C. gemellata* and *C. hyperici* thus formed an important item in the diet of many birds, the overall losses suffered by the beetles could not have been high. It was a common experience at this time of year to find large numbers of birds feeding on scattered beetles near the forest margin, and ignoring enormous concentrations of them only 75-100 yd. away from the trees. Few birds ranged far from tree and shrub cover during the spring nesting period. Where large concentrations of adult beetles occurred within the hunting range of most birds in an area, the numbers of the latter were invariably too low to destroy more than a small fraction of the insects.

High mortalities occurred only where the beetle population was of relatively low density and restricted to a small area close to trees. Mortalities of the order of 50 per cent. or higher were observed in such areas during the springs of 1948 and 1949, before the seasonal temperatures were high enough to cause much mortality or flight. In each instance the beetles had formed small feeding fronts. These were attacked daily by flocks of *Strepera* and *Corcorax* and numerous nesting pairs of other species, e.g. *Pachycephala.* The presence of dozens of crop pellets of *Strepera,* each containing the remains of over 50 beetles, and the droppings of other birds showed that thousands of the insects had been destroyed by these predators.

(ii) *By Other Animals.*—Apart from stock, which sometimes either trampled or fed on the weed, the only other animals actually observed to destroy *Chrysomela* eggs were the larvae of *C. gemellata* and *C. hyperici* themselves. They were never seen to eat eggs; but, when short of food, sometimes bit jagged holes in them. Some unknown predator caused egg losses to *C. gemellata* amounting to 1-2 per cent. of the total production in nine of the 30 study areas used for intensive work. The damaged eggs, which did not collapse, all had a small round hole pierced towards one end through which up to half the contents had apparently been sucked.

Predation on the active stages of *C. gemellata* and *C. hyperici* was observed infrequently although much time was spent in observations on the feeding and hunting habits of the polyphagous insect and arachnid predators present in the study areas. Unfortunately, some were nocturnal in habit and could not be watched satisfactorily. The ant *Chalcoponera cristulata* Forel appeared to be the principal predator of *Chrysomela* larvae. The only other insect seen to feed on the larvae was an unidentified staphylinid. Suspected predators include the carabid beetles, *Sarticus esmeraldipennis* Cast. and *Diaphoromerus germari* Cast., and the lycosid spiders, *L. pictiventris* L.Koch, *L. godeffroyi* L.Koch, and a possible new species of *Lycosa.* These predators, which were frequently active during the winter, lived not only in places containing plenty of other prey, but also in some study areas in which *Chrysomela* larvae appeared to be the only source of food.

In general, the numbers of *Chalcoponera* and other polyphagous predators were too low to have destroyed a large proportion of the *Chrysomela* larvae. The predators were most numerous in and near eucalypt forests. In two forest study areas heavy larval losses occurred, which could only be accounted for by predation*. (In the other forest sites egg dislodgment obscured the picture.) In both areas *Chalcoponera* was very numerous, and hunting occurred throughout the winter.

The results of population counts made in these areas are shown in Table 22, in which comparable figures are given for other areas in which few potential predators were present. For *C. gemellata* the comparison had to be limited to the single forest area (1*c*) in which numbers suitable for sampling occurred, area 2*c* in a pine plantation on the same aspect of the same hillside, and a treeless area *x* (two study areas combined) situated about 300 yd. from area 1*c*. The significant feature of the count results is that the low-density larval population in area 1*c* dwindled and vanished; whereas some individuals reached the fourth instar and entered the soil in areas 2*c* and *x*. For *C. hyperici,* an additional pair of study areas was available, the forest site 3*c* and an adjacent treeless area 1*a*. The results again showed a much lower larval survival in the forest areas. It was concluded that predation was largely responsible for the site differences in larval survival.

During the spring feeding period the adult beetles were attacked sometimes by *Harpobittacus tillyardi* E.P. (Bittacidae), *Oechalia schellembergii* Guer. (Pentatomidae), *Iridomyrmex detectus* Sm. (Formicidae), and spiders (*Lycosa* spp. and *Araneus* sp.). The numbers of these polyphagous predators were so low in relation to *Chrysomela* numbers at this time of the year that the proportions destroyed were undoubtedly small. After being virtually free from predation during the aestivation period, the adult beetles were attacked again during the reproductive period by *Iridomyrmex,* lycosids, and an unidentified asilid. At this time the numbers of *Chrysomela* adults were relatively low, and the percentage destroyed may have been considerably higher than during the spring. As for the larval stage, the losses appeared to be greatest in and near forest areas, where *Iridomyrmex* was numerous. This ant appeared to ignore the *Chrysomela* larvae, but collected both dead and living adults in places where the author had difficulty in finding them.

(*e*) *Insect Parasitism*

No insect parasites were found in the thousands of eggs taken from the field and allowed to complete development in the laboratory. Only one parasitized adult beetle was ever found. This was a *C. gemellata* male which contained two dipterous larvae (Tachinidae?). The only insect found to parasitize larvae of *C. gemellata* and *C. hyperici* was a species of *Froggattimyia* Townsend (Tachinidae), either *F. tillyardi* Mall. or a new species. *Froggattimyia* normally parasitizes the chrysomelid *Paropsis.* The members of this large genus feed on eucalypts and acacias.

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* Other possible causes of mortality tested experimentally included: winter temperatures; the type of foliage available as food; and the possible "trap" effect of the large amount of leaf and twig debris on the ground surface. None had a significant effect on larval numbers.

Parasitized larvae of *C. gemellata* and *C. hyperici* survived in the field until shortly before pupation. The parasite pupated in the host larvae after they had entered the soil. During 1949, the proportion of parasitized larvae in population samples from the study areas never exceeded 1 per cent. for *C. gemellata* and 3 per cent. for *C. hyperici.* No evidence of parasitism was found in 11 of the 15 areas from which larvae were collected and dissected. The following year parasitized larvae were found only in samples of *C. hyperici* from forest areas, the maximum percentage recorded being 15. Thus considerable numbers of this beetle are sometimes destroyed by the parasite in the areas where individuals of the related *Paropsis* spp. are numerous.

(*f*) *Starvation*

It remains to consider the effect of exhaustion of the available food supply on the larvae and adults of *C. gemellata* and *C. hyperici.* In habitats in which pure or mixed populations of the beetles could maintain themselves unaided by the repeated immigration of adults, numbers invariably increased until the larval population density was high enough to cause complete defoliation of the host plant over extensive areas. In all known instances of complete defoliation some larvae of one or both species survived to pupate and produce adult beetles. These consumed any regrowth made by the damaged *Hypericum* and then wandered about in all directions in search of more food. The proportion surviving depended on the proximity of further supplies of food and the amount of destruction caused by temperature etc. in the absence of protective *Hypericum* foliage. Field experiments, in which adult beetles were confined in wire-gauze cages similar to those described in Section VII, indicated that roughly 50 per cent. of the adults of each species could survive starvation for 4-5 weeks during the winter or spring, providing conditions were otherwise favourable. However, when extensive areas of the weed were first defoliated by larvae, few of the adults produced succeeded in reaching further supplies of food unless they occurred within approximately 2-3 ch. of the insects. Widespread defoliation of the host plant not infrequently resulted in the complete destruction of *Chrysomela* populations.

The following observational trial was carried out on a population of *C. gemellata* in 1949 to obtain some idea of the proportion of larvae destroyed by starvation. Eight small plots, each approximately 10 sq. yd. in area, were selected at random in an area of 1 sq. ch. where the dense growth of *Hypericum* had been almost completely defoliated before the end of April, an unusual occurrence associated with very early oviposition and hatching. Population numbers were sampled at intervals by counting the number of individuals in three 1 by 1 lk. quadrats placed at random in each plot. Apart from a negligible number of eggs, just about to hatch, the initial population was composed of first-, second-, third-, and fourth-instar larvae in the approximate proportions of 1:6:9:10 respectively.

Table 23 shows the decrease in population that occurred between April 29 and September 1 in the sampling area. Direct observation showed that the larval mortality was due almost entirely to three factors: starvation, frost, and predation by birds, notably *Strepera versicolor*, a flock of which visited the area daily. The numbers of larvae above ground decreased partly as the result of mortality and partly because some entered the soil prior to pupation. It will be noted that a few larvae survived above ground for approximately 2 months, and that the number of individuals in the soil changed very little between May 16 and June 20. The emergence of adult beetles from the soil began about June 13. All had emerged by September 1 when the ground surface was littered with their dead bodies. The estimated percentage mortality for the period April 29 to May 30, i.e. before the situation was complicated by adult emergence, was 51 per cent. (confidence limits at the 5 per cent. level ± 16.06).

TABLE 23

DECREASE OF A *C. GEMELLATA* POPULATION IN AN AREA WHERE *HYPERICUM* WAS COMPLETELY DEFOLIATED (1949)

Total individuals per 24 sq. lk.

Sampling Date	State of Weed	Larvae Above Ground	Larvae In Soil	Pupae In Soil	Young Adults	Total In Soil	Grand Total
Apr. 29	Almost defoliated	653	0	0	0	0	653
May 9	Completely defoliated	493	132	19	0	151	644
May 16	Completely defoliated	196	180	57	0	237	433
May 30	Completely defoliated	71	178	64	7	249	320
June 13	Completely defoliated	17	144	57	13*	209	231
June 20	Completely defoliated	13	152	52	7*	206	224
July 1	Completely defoliated	3	134	34	22*	190	193
Sept. 1	Completely defoliated	0	0	0	0	0	0

* Some adults had emerged from the soil.

Direct observation indicated that the vast majority of individuals that had entered the soil by May 16 survived until they reached the adult stage, i.e. approximately one-third of the total population. These individuals succumbed either to continued starvation or to frosts, as the birds had left the area. A similar trial carried out in 1950 on a larval population of *C. gemellata*, approximately three times as dense initially, indicated that only 2 per cent. reached the adult stage. Apparently the intraspecific competition for food had a more severe effect at the higher density.

Immediately after the first population count made in the 1949 trial, larvae were collected from the partially defoliated plants around the sampling plots and taken to the laboratory. There they were divided into eight lots of 52 individuals, each being composed of larval instars in the same proportions as they occurred in the sampling area. Each group of larvae was placed on moist blotting paper in a large glass jar, the mouth of which was covered by cheesecloth to prevent escapes. Four lots of larvae were fed daily and the other four starved. The jars were arranged in pairs, consisting of one fed lot and one starved lot, and kept at room temperatures fluctuating between 35 and 70°F. After correction for the few deaths that occurred in the controls by Abbot's formula (1925), the estimated mean mortality over the period April 30 to May 30, attributable to starvation, was 43 per cent. (confidence limits at the 5 per cent. level ± 11.80). This result is not significantly different from that of 51 per cent. recorded for the same period in the field. It is reasonable to conclude that starvation alone would have caused a mortality in the sampling area similar to that due to all three of the destructive factors operating, i.e. would have eliminated approximately half the population within a month. This result is similar to that obtained for both immature and reproducing adults in field experiments.

The 1949 field trial serves to illustrate the important point that larvae of *C. gemellata,* when in high numbers, can defoliate the host plant completely in May, June, or July. This means that the species has a decided advantage over *C. hyperici* in competition for food. Most eggs of the latter do not hatch until late July or August (Section IV). In several large observation areas *C. hyperici* was eliminated completely as a result of defoliation by *C. gemellata,* occurring either before any eggs of the former had hatched or before any larvae of it had reached the third instar. On each occasion only a small proportion of the *C. gemellata* adults produced survived to reach further supplies of food.

X. SIGNIFICANCE OF THE FACTORS REDUCING POPULATION NUMBERS

Destruction of food and reduction of protective cover appeared to be the only controlling or density-dependent factors* affecting the numbers of *C. gemellata* and *C. hyperici* in the Bright district. It so happens that the food of these insects also constitutes an important part of their protective cover in treeless areas. When they had consumed the food around them, the insects were automatically exposed to the intensified action of destructive factors, essentially density-independent in nature (see below). In the larval stage, these factors were largely redundant as most individuals destroyed by them would have succumbed to starvation. This did not always apply to the adult stage. Because of their greater mobility the adults had a better chance of reaching further supplies of food at a distance. The proportions reaching such food were sometimes limited greatly by the destruction caused by high temperatures etc., which followed removal of the protective foliage.

Where other factors permitted the multiplication of the two species for a number of generations, side by side, *C. hyperici* was sometimes eliminated completely by interspecific competition for food. However, the overall rate of increase of *C. gemellata* in the total area favouring both species was not much greater than that of *C. hyperici* during the study period. This was due mainly to the fact that *C. gemellata* itself usually suffered very severe losses after consuming the local food supply, and sometimes even died out completely.

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* Terms used in the sense of Nicholson (1933) and Smith (1935) respectively.

In many places the population increase of each species to the maximum set by food supply was prevented by density-independent mortality and, in timbered areas, by density-independent migration as well. Singly, or in combination, these factors eliminated both species either annually or within 2-3 years of recolonization.

Intensive field studies, together with extensive, less detailed observations, suggested that, *where the host plant retained most of its foliage*, the principal factors reducing population numbers in the three main types of habitat were those in Table 24.

Habitats of type (*a*) which included dense wort habitats and others in which a considerable proportion of the total cover was provided by densely growing perennial grasses, e.g. *Themeda australis* (R.Br.) Stapf., were the most favourable for both *C. gemellata* and *C. hyperici*. In them, each species was able to increase, within 4-6 years, from low numbers to a density high enough to cause complete defoliation of the host plant. As a result, the population was eliminated by mortality and emigration. Subsequent recolonization depended on:

(i) Whether or not the host plant managed to recover.
(ii) The proximity of other populations of the insects.
(iii) The ability of the insects to re-establish themselves in the frequent absence, for one or more years, of a large amount of protective cover—available originally in the form of mature *Hypericum* and undecomposed *Hypericum* debris.

In most habitats of type (*b*), e.g. stony dredgings, the insects were eliminated at frequent intervals, mainly by frosts during the winter and by over-heating during the summer. Consequently, they have increased to the population maximum set by food supply much less frequently than in treeless areas containing more cover.

Because of high mortality (*C. hyperici* particularly) and behaviour responses causing the adult beetles to avoid remaining in timbered areas (*C. gemellata* particularly), neither insect has been able to colonize habitats of type (*c*) successfully. Except in a few instances in which *C. hyperici* has managed to multiply to the limit determined by food, and a single case in which *C. gemellata* did likewise, the host plant has suffered complete defoliation for only short periods from the brief attacks of adult beetles forced into timbered areas by lack of food outside.

XI. EFFECT OF THE INSECTS ON THEIR HOST PLANT

(*a*) *Characteristics of* Hypericum

Undisturbed stands of *Hypericum* are maintained by the production of suckers, developed mainly from the lateral roots. An individual plant may be represented by a single crown or by as many as 12 attached to the same root system. The life of individual crowns and the rate and amount of vegetative reproduction depend on soil conditions and the presence or absence of competing root systems of other plants (Clark and Clark 1952; Nancy Clark, unpublished data*). Two principal types of wort stand may be recognized:

(i) Those in which the crowns survive for 3 years or more and reach a comparatively large size. Frequently the crowns die out in patches, and occasionally *en masse*, before much suckering occurs. Such stands are present where conditions favour the development of deep vertical roots, e.g. many areas of farmland. The associated flora consists mainly of stunted annuals and mosses. These stands provide most of the dense wort habitats of the beetles.

TABLE 24

FACTORS REDUCING POPULATIONS

Period of Life Cycle	(*a*) Treeless Areas with Much Cover	(*b*) Treeless Areas with Little Cover	(*c*) Eucalypt Forests and Pine Plantations
Oviposition to adult emergence	1. Frost 2. Soil moisture 3. Egg dislodgment and fungal attack 4. Predation [*Heavy losses*]	As for (*a*) [*Elimination occasional*]	1. Egg dislodgment and fungal attack 2. Soil moisture 3. Predation (forests only) [*Heavy losses, elimination occasional*]
Adult feeding period in spring	Predation [*Light-moderate losses*]	As for (*a*)	1. Emigration 2. Predation (forests only) [*Elimination frequent*]
Aestivation period of adults	1. Desiccation 2. High temperatures [*Heavy losses*]	1. High temperatures 2. Desiccation [*Elimination frequent*]	Desiccation [*Light-heavy losses*]
Reproductive period of adults	1. Predation 2. Frosts (*C. hyperici* only) [*Heavy losses*]	As for (*a*)	1. Emigration 2. Predation (forests only) [*Elimination frequent*]

(ii) Those in which most crowns die in less than 3 years. The crowns differ from those in (i) by being smaller and by possessing a strongly developed system of lateral roots. Suckering is an almost continuous process and the crown density is generally higher than in (i). Such stands occur on shallow or stony soils, and on better soils where competing plants are abundant, e.g. *Themeda.* The extreme example of the type occurs in eucalypt forest where suckering is so vigorous that a wort plant is usually composed of a number of crowns. In treeless areas, these stands provide a few dense wort habitats and all of the sparse wort habitats of the beetles.

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* A paper on the biology of St. John's wort in the Ovens Valley, Victoria, with particular reference to entomological control, is in preparation.

Stands of type (i) were less resistant to defoliation by the insects than those of type (ii). This was due apparently to the much smaller amount of suckering and the associated predominance of large, old crowns. The most resistant stands of all were those in eucalypt forests. They could not be destroyed effectively by hand defoliation sustained for longer periods than the insects are able to maintain the process (Nancy Clark, unpublished data). Thus the stands most resistant to defoliation occurred in the places least favourable for colonization by the insects. The most susceptible stands were those in pine plantations where the weed was weakened greatly, and ultimately killed, by tree shade.

The presence of a germination inhibitor in the sticky secretion coating the seeds of *Hypericum* gives the weed a chance to recolonize an area for at least 6 years after destruction of the original stand. Generally one or more crops of seedlings appear annually in well-illuminated sites after the original stand has been destroyed, but the mortality is usually high. Re-establishment from seed may be prevented for a year or more by the occurrence of moisture conditions unfavourable for seedling survival during the germination period, September-April. Under favourable conditions, a dense stand of mature *Hypericum* can develop in 2 years.

(*b*) *Influence of Other Plants on* Hypericum

(i) *Mature* Hypericum.—Apart from pine trees, certain other trees, and tall, densely growing shrubs, the only plants observed to have any deleterious effect on mature *Hypericum* were perennial grasses. Davey (1917, 1919, 1922) has described the destruction of well-established stands of wort by *Themeda australis* and other perennial grasses when rabbits and stock were excluded. The author has observed that, under light-moderate grazing, such grasses limited the size and life of wort crowns, but usually failed to prevent suckering and re-establishment. *Hemarthria uncinata* R.Br., an unpalatable mat grass, was the only species observed to eliminate undefoliated mature *Hypericum* during the study period. In this case, the interspecific competition was probably for both light and moisture.

These grasses grew in abundance with *Hypericum* only in a few areas of farmland, railway enclosures, and certain forest types—as a result of the land-use methods practised in the district (Nancy Clark, unpublished data). Consequently, an outstanding feature of the wort infestations was the frequent absence of associated species capable of competing effectively with mature wort plants. Thus, unless a very high percentage of the plants in a stand was destroyed by the insects, suckering by the survivors frequently resulted in the reoccupation of spaces left vacant by deaths in a very short time (Clark and Clark 1952).

(ii) *Seedling* Hypericum.—The young seedling of *Hypericum* is readily destroyed by shading. Any plant, or combination of plants, capable of producing an almost complete shade can effectively prevent the regeneration of the weed from seed. The winter-growing annual clover, *Trifolium subterraneum* L., is a particularly effective species in this regard (Moore and Cashmore 1942). Other effective species are *Themeda australis, Danthonia penicillata* (Labill.) F. Muell., *Bromus mollis* L., *Plantago lanceolata* L., *Hypochoeris radicata* L., etc. The âmount of effective cover produced by most of these species depends on the extent to which they are grazed by stock. Introduced fodder plants like subterranean clover usually require annual applications of superphosphate to produce the necessary cover and shade. In areas of farmland where such plants grow naturally in association with stands of *Hypericum*, or can be established successfully, the weed has been controlled effectively by destroying the mature wort plants by means of the beetles. Suitable grazing management, aided, where necessary, by applications of superphosphate, distribution of pasture seed, etc., has prevented the regeneration of *Hypericum* from seed. Most of the seedlings that escaped destruction by shading were consumed inadvertently by stock. In such places, grazing animals have replaced the insects as defoliators of *Hypericum*. They have virtually ceased to provide habitats for the beetles.

Shade-producing herbs of the type listed cannot effectively colonize many areas of stony soils, even in the absence of mature *Hypericum*, e.g. dredgings. Thus the degree of control obtained in such places depends entirely on the insects.

(*c*) *The Ability of the Insects to Destroy Mature* Hypericum

The growing period of *Hypericum* is longer than the feeding period of each insect. In order to kill healthy, mature wort plants, the chrysomelids had to keep them in an almost leafless condition for several months. Complete defoliation for shorter periods, or partial defoliation for longer periods, even if repeated annually, killed very few healthy wort plants. Frequently, destruction operated on the "hit or miss" principle; either because the insects failed to return the year after complete defoliation first occurred (except perhaps for a brief period), or because stands increased in resistance as a result of the suckering stimulated by previous defoliation (Clark and Clark 1952).

Where high *Chrysomela* numbers developed, the wort plants were usually first denuded of foliage and softer stems by the larvae during the winter or early spring. They fed on the procumbent autumn-winter growth and later consumed the fertile shoots as they appeared (usually August). Generally many plants survived this damage and produced some regrowth while the insects were pupating. Defoliation was continued by the adult beetles when they emerged from pupation later in the spring. These consumed the regrowth, leaving only the tougher parts of the stems, and moved off in search of more food. Where other infestations occurred within 2-3 ch. of the defoliated site, the adult beetles accumulated on the nearest plants to form feeding fronts, which progressed slowly through stands, leaving a trail of defoliated plants behind them (Clark and Clark 1952; Wilson and Campbell 1943). Except in pine plantations, the spectacular attack of the adults killed very few previously undamaged wort plants, and complete defoliation by the larvae was necessary to cause large-scale destruction.

A study of the effect of *C. hyperici* on *Hypericum* in the Mannus Valley, New South Wales (Clark and Clark 1952), showed clearly that this insect has only a limited ability to kill mature wort plants. More extensive observations at Bright showed that the species is really effective only in stands characterized by large, relatively old wort crowns and limited suckering. On the other hand, *C. gemellata* was capable of killing out all types of stand occurring in treeless areas when conditions favoured multiplication to high numbers. This difference in effectiveness was associated with the principal difference in the seasonal cycles of the insects (see Section IV). As its larvae appeared earlier each year than those of *C. hyperici, C. gemellata* was able to keep the host plant in an almost leafless condition for 4-6 months. *C. hyperici* was able to sustain defoliation for only 2-3 months. Usually the insects occurred in mixed populations, and mixtures in which *C. hyperici* predominated were frequently less effective in stand destruction than those in which *C. gemellata* was the more numerous species. Although *C. hyperici* has undoubtedly contributed to the wort destruction observed to date, it is probable that *C. gemellata* alone would have been practically as effective as the two species in combination.

(*d*) *The Ability of the Insects to Control Regeneration from Seed*

Owing to the insects' poor powers of dispersal and the operation of numerous unfavourable factors in the environment, their return to deal with the seedling regrowth, which followed destruction of the original stand, has occurred in a haphazard manner (cf. Wilson and Campbell 1943). The insects have returned annually to some areas: they have not returned to others after 5 years. Frequently, after returning, they have died out as a result of starvation or frosts long before the reservoir of wort seed was exhausted, giving the weed a further chance to recover.

In certain treeless areas, where other controlling factors are lacking, the weed is frequently able to reach maturity at a density not much lower than that occurring originally before being attacked heavily again. In such areas, the overall picture is one of violent density fluctuations in time and space on the part of the insects and their host plant. The insects have either reached, or are close to reaching, a state of balance with the weed without reducing it greatly in quantity.

The "dislike" of the adult beetles for timbered sites has resulted in the effective control of seedling regeneration in small treeless areas close to the margins of wort-infested forests, scrubs, and plantations. *C. gemellata* has been more effective in this regard than *C. hyperici* (Section VI(*d*)). The process of control may be described as follows:

(i) The wort stand in a treeless area near dense timber was first defoliated by larvae and adults in the usual manner and largely detroyed.

(ii) After the formation of feeding fronts, the adult beetles were eventually forced to enter the timbered area for food.

(iii) After the spring feeding period, some adults aestivated either within or at the margin of the timbered area.

(iv) After aestivation, nearly all *C. gemellata* adults and a variable proportion of *C. hyperici* adults left the immediate vicinity of the trees and oviposited on the regrowth of *Hypericum* produced from seed etc. in the adjacent treeless area. Large numbers of eggs, mainly *C. gemellata,* were thus distributed within a zone several chains wide beside the trees.

(v) After defoliation and destruction of practically all the regrowth occurring within the zone by larvae and adults, some of the surviving beetles again aestivated close to the tree boundary.

(vi) Many adults returned again the following year to oviposit on the next crop of seedlings.

This movement of beetles to and from the forest margin was first observed in Baker's Gully in 1948-49. Approximately 4 years previously, the dense wort in a cleared paddock, almost surrounded by trees, had been practically killed out by a mixed population of the beetles in which *C. gemellata* predominated. The subsequent regeneration over a total area of 5 acres had apparently been destroyed each year as only a few young plants and seedlings were present in April 1948. (Shade-producing herbs were very scarce in the paddock.) Effective control, actually observed in 1948 and 1949, continued until 1950 when the paddock was cultivated and observations ceased. During 1949 and 1950 this type of control, involving a timbered "barrier" zone infested with *Hypericum,* was observed in several other places, namely Freeburgh, Porepunkah, and Buckland. It appears to be gradually extending along the treeline adjoining the cleared portions of the valleys, the degree of control decreasing as the distance from the trees increases. It is unlikely that the insects will operate with similar efficiency in all such areas as the annual occurrence of adequate food for the relatively immobile larval stages is partly a matter of chance. Also, there is the possibility of elimination by frosts etc.

As the areas involved are small, this example of effective entomological control is not of much practical importance. It is, however, of considerable scientific interest. The presence of an area tolerated for an inactive period of the life cycle, but avoided when possible for ordinary activities, adjoining an area favoured for these activities, has enabled the insects to persist in moderate numbers where they would otherwise have been eliminated for a period of up to 5 years. The timbered area has acted as a damping factor to population fluctuation.

XII. Acknowledgments

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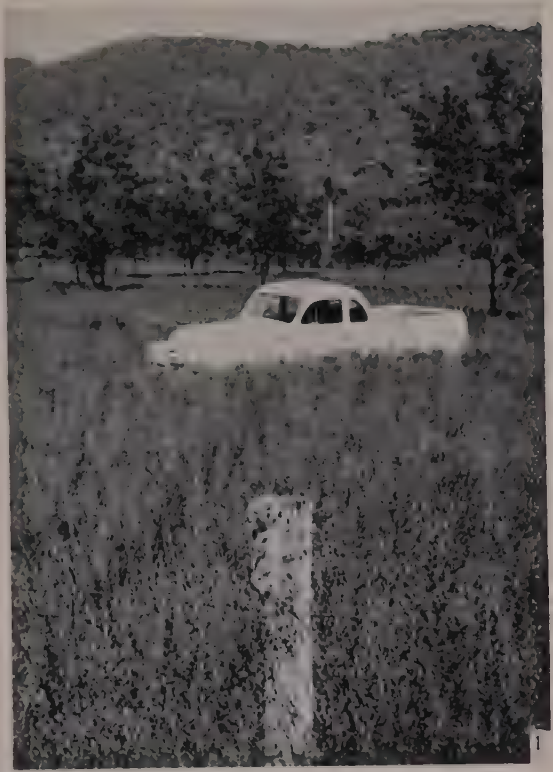


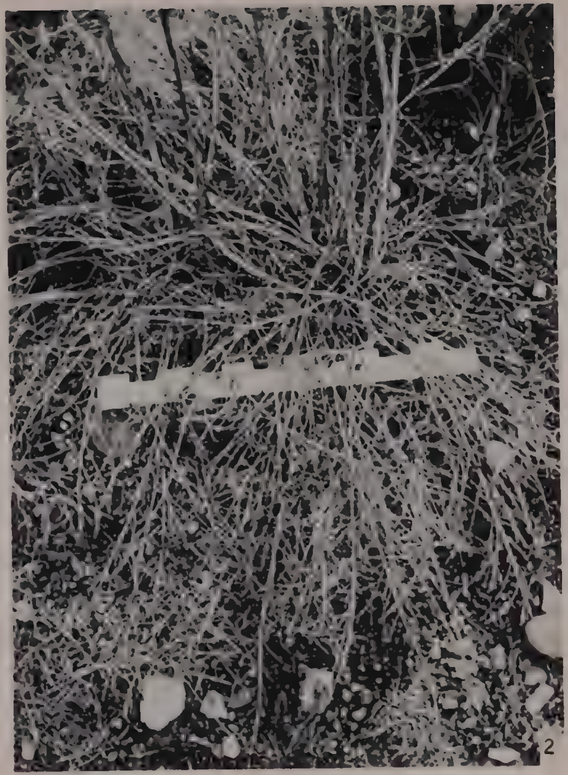
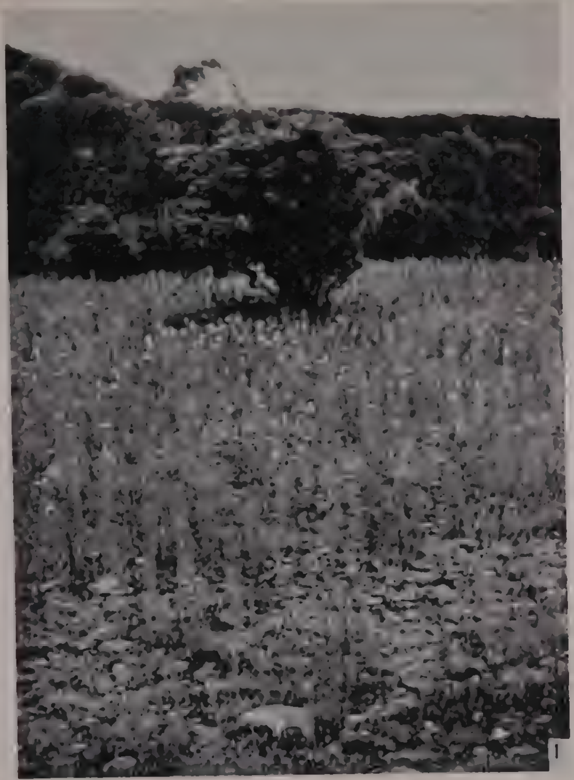


Fig. 1.—Dense stand of *Hypericum* in abandoned farmland. The photograph was taken during the winter, after the erect, fertile stems had begun to dry off and lose their leaves.

Fig. 2.—Close-up of a single wort plant in a dense stand similar to that in Figure 1. The photograph was taken late in the winter, after chrysomelid larvae had completely defoliated the mat of procumbent, autumn-winter growth. Note the length and density of the procumbent stems (ruler 12 in. long).



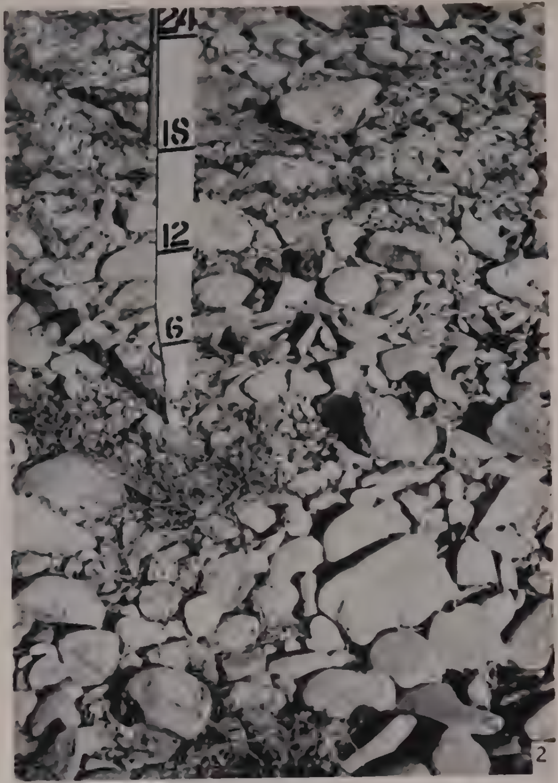
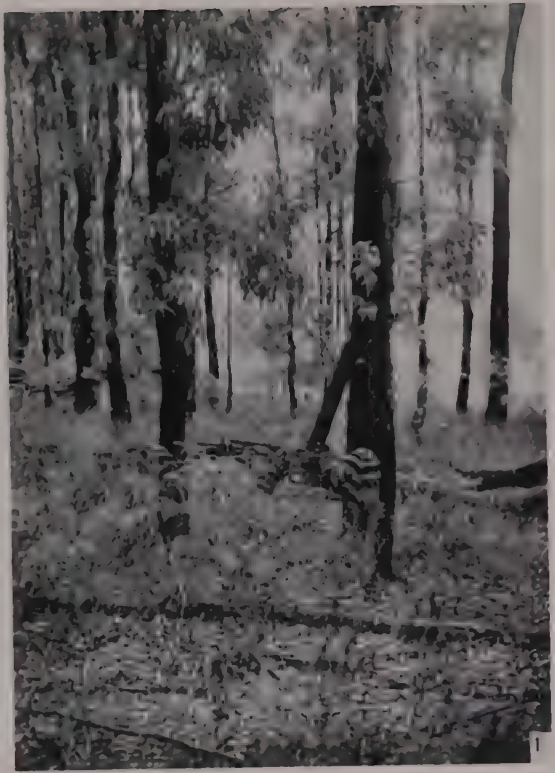


Fig. 1.—Stand of *Hypericum* on gold dredgings, taken late in the spring, soon after flowering began. The plants averaged 15 in. high. Note relative sparseness of growth and the stony surface of the area.

Fig. 2.—Close-up of a wort plant on stony dredgings, after partial defoliation by chrysomelid larvae. The indicator post is graduated in inches. Compare size of mat with that in Plate 1, Figure 2.



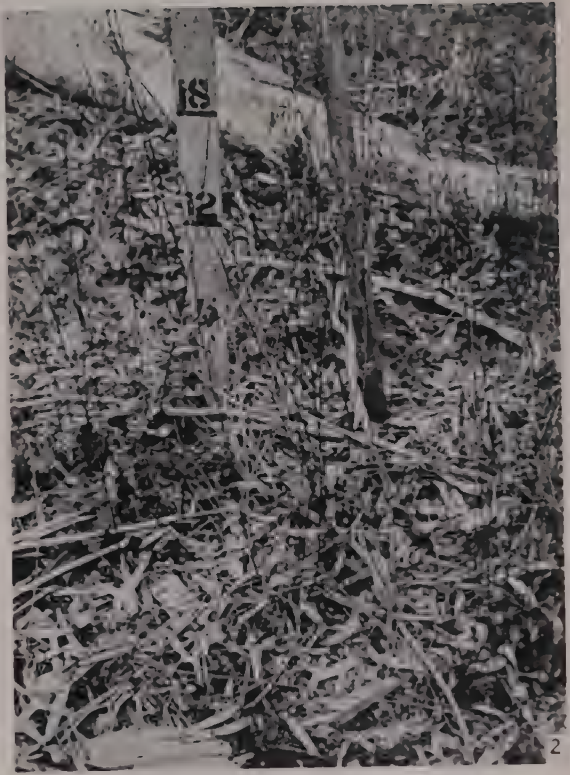


Fig. 1.—Typical growth of *Hypericum* in eucalypt forest. The photograph was taken after the erect fertile stems had shed their leaves to facilitate comparison of the density of weed growth with that in Plate 1, Figure 1.

Fig. 2.—Close-up taken in the same area. Note the large mount of plant litter on the soil surface.

APPENDIX I

ON ESTIMATION OF THE NUMBER OF EGGS OF C. HYPERICI IN A MIXED SAMPLE OF EGGS OF C. HYPERICI AND C. GEMELLATA

By G. A. McINTYRE

Let a be the probability that an egg of *C. hyperici* will be equal to or less than 10 micrometer units in width and b be the similar probability for an egg of *C. gemellata*. If x is the number of *C. hyperici* eggs in a sample of N eggs, then $N-x$ is the number of *C. gemellata* eggs. Let z be the total number of eggs with widths equal to or less than 10 micrometer units. With simple random sampling z is then distributed as the sum of weighted binomial variates, with an expectation of $ax+b(N-x)$ and variance $a(1-a)x+b(1-b)(N-x)$. If x is estimated as $\hat{x}=z-bN/(a-b)$ then for constant x the expectation of $\hat{x}$ is x and the variance of $\hat{x}$ is

$$\frac{a(1-a)x+b(1-b)(N-x)}{(a-b)^2}. \quad \ldots \quad \ldots \quad \ldots \quad (1)$$

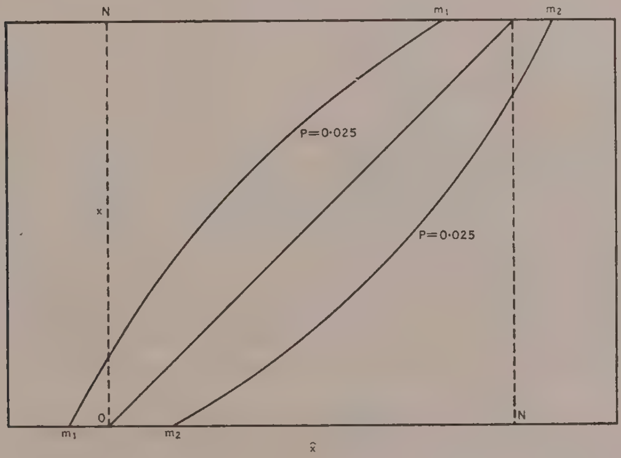


Fig. 3.—Diagrammatic representation of confidence intervals of x for given $\hat{x}$ $(a+b=1)$.

With large numbers so that the effect of discontinuity due to discrete increments is small, the relation between x and $\hat{x}$ for constant N may be represented as in Figure 3, fiducial limits at a specified probability level to x being given for particular values of $\hat{x}$. The lower limit to x for $\hat{x}$ between M_1 and M_2 is zero with certainty and correspondingly for the upper limit with $x=N$.

The exact form of the distribution of $\hat{x}$, given a, b, N, and x, is determinable, but the estimation of limits will usually be adequately determined by assuming normality.

It may be noted that for given x and N the variance of $\hat{x}$ is a function of a and b which are determined by the limit chosen. Evidently the limit that will give minimum variance for $\hat{x}$ is dependent on the ratio $(N-x)/x$, so that there is some arbitrariness in the selection of a fixed limit to apply to all values of this ratio.

Provided that the population distributions are such that overlap exists over the whole range of values of the variable, then if the ratio $(N-x)/x$ is k the limit for minimum variance is defined by $a+kb=(k+1)/2$. In the event of the frequencies of one distribution becoming zero as the variable changes while for the other they remain finite, the limit for minimum variance as k changes cannot pass beyond the point of extinction of the first distribution. For the particular case of $k=1$ the minimum variance is defined by $a+b=1$, i.e. with equal numbers of the two species, the proportion above the limit for the species with the smaller eggs should equal the proportion below the limit for the species with the larger eggs. With complete separation of the population distributions any point in the region separating the distributions will satisfy this requirement, and the contiguous boundary values of the two distributions will be the limits for minimum variance whatever the value of k. In general, for reasons of symmetry, it would seem best to adhere to the limit defined by $a+b=1$ unless dealing with mixed populations known to be consistently dominant in one of the species.

To this point it has been assumed that a and b are known exactly and that simple random sampling applies. In practice, a and b are known only through sampling and simple sampling would rarely operate. The variability in estimate may be approached from a slightly different angle. In any specific instance $z=a'x+b'(N-x)$ where a' and b' are the actual proportions at or below the boundary for the two species, so that $x=(z-b'N)/(a'-b')$. Now a' and b' are unknown except that they are probably independent variates about the means a and b. If then x is estimated as $(z-bN)/(a-b)$, the fiducial distribution of x has an approximate variance, ignoring second order terms, of

$$\frac{\sigma^2 a'(z-Nb)^2+\sigma^2 b'(z-Na)^2}{(a-b)^4}. \quad \ldots \quad \ldots \quad \ldots \quad (\mathbf{2})$$

This may be derived from (**1**), substituting with z for x.

The variates a' and b' may each be regarded as the sums of three separate components:

(1) The general value of the proportion equal to or less than 10 micrometer units in all samples of the species, with presumably equal proportions at each stage of development. (A sampling error may be attached to the estimation of it.)

(2) The deviation from the general mean of the proportion equal to or less than 10 units in width in the subpopulation from which the sample was taken.

(3) The binomial deviation in the actual proportion in the sample from the mean proportion equal to or less than 10 units in width in the subpopulation.

TABLE 25

RESULTS OF ANALYSES OF VARIANCE AND χ^2 TESTS MADE ON THE MEASUREMENTS OF EGG WIDTH IN *C. HYPERICI* AND *C. GEMELLATA* GIVEN IN TABLES 1 AND 2

	Analysis of Variance (in ½ micrometer units)				
	Degrees of Freedom	Sum of Squares	Mean Square	F	Significance
(i) *C. hyperici*					
Samples	14	92.5	6.61	6.42	$P < 0.001$
Within samples	735	755	1.03		
	χ^2 (14 d.f.) $= 15.62$, $P = 0.5$				
(ii) *C. gemellata*					
Samples	14	142.2	10.16	10.6	$P < 0.001$
Within samples	735	763	0.96		
	χ^2 (14 d.f.) $= 42.14$, $P = < 0.001$				

Analyses of variance on the measurement data of Tables 1 and 2 revealed heterogeneity between the samples for both species (Table 25). On the other hand, while χ^2 for the 2×15 table for *C. gemellata* (each sample distribution being classified into widths exceeding 10 units and the remainder) was highly significant, the corresponding value for *C. hyperici* was not. The variances of sample means would lead one to anticipate higher values for χ^2 in both species. The distributions for the two species were remarkably similar with *C. hyperici* displaced downwards by approximately one micrometer unit relative to *C. gemellata.* Accordingly, the view has been taken that the variation in the proportion above 11.0 units in *C. gemellata* could be taken as replicate variation for *C. hyperici* above 10.0 units. The χ^2 value for the sectioning of the samples of *C. gemellata* at 11.0 is 93.3. The corresponding χ^2 for the sample variation in the proportion at or below 9.0 units in *C. hyperici* is 81.8. The pooled χ^2 for the sectioning of *C. gemellata* at 11.0 and *C. hyperici* at 10.0 is 108.9 for 28 degrees of freedom, the ratio of the experimental value to the expected being 3.9. The corresponding ratio of pooled χ^2 ($= 123.9$) for the sectioning of *C. gemellata* at 10.0 and *C. hyperici* at 9.0 is 4.4.

This would mean that the variance in the mean proportion for a sample of 50 eggs of *C. hyperici* due to binomial variation is 1/2.9 of the variance due to real differences in the proportion at or below the selected limit of 10.0 in the populations sampled. Similarly the ratio of the variances due to binomial variation and population differences for *C. gemellata* is 1/3.4.

It is now possible to estimate the variances of the separate components of a' and b'. These are:

C. hyperici	*C. gemellata*
(1) $3.9 \times \frac{0.129 \times 0.871}{750} = 0.00058$	(1) $4.4 \times \frac{0.779 \times 0.221}{750} = 0.00101$
(2) $2.9 \times \frac{0.129 \times 0.871}{50} = 0.00651$	(2) $3.4 \times \frac{0.779 \times 0.221}{50} = 0.01171$
(3) approx. $\frac{0.129 \times 0.871}{\hat{x}}$	(3) approx. $\frac{0.779 \times 0.221}{N - \hat{x}}$

Example: Suppose a composite of samples No. 15 (Tables 1 and 2) for *C. hyperici* and *C. gemellata* is presented, and the fact that they have contributed to the estimation of a and b is ignored.

Then $N = 100$, $z = 59$, $\hat{x} = (59 - 22)/65 = 56.9$ $(x = 50)$.
Var. $a' = 0.00907$, var. $b' = 0.01671$.
Variance $\hat{x} = 143.14$, standard error $\hat{x} = 11.97$.

Fiducial limits to x are 56.9 ± 23.5, at the 5 per cent. level.

APPENDIX II

DETAILED DESCRIPTION OF THE METHODS USED FOR THE ESTIMATION OF EGG NUMBERS IN THE FIELD

(*a*) *In* 1949

(i) *C. gemellata.*—The 1949 population study was originally intended as a preliminary investigation, and it was planned to make more precise and extensive studies the following year. However, for several reasons it was not possible to obtain many suitable study areas in 1950. It therefore became necessary to make the fullest possible use of the data obtained in 1949. This led to improvisations in method. The first procedure was used to estimate the total egg production of *C. gemellata* in the study areas. This method required the use of data on time of egg development under different temperature conditions, obtained from the type sites, to estimate incubation periods in corresponding study areas. However, few observations were made in the type sites during 1949 (see Section V). In order to have data on time of egg development covering the whole oviposition period it was necessary to combine the 1949 results with those obtained in the type sites in 1950. The only complete daily temperature records for the oviposition periods of both years were those provided by a thermograph in a standard meteorological screen situated approximately 50 yd. from the type sites. It was therefore necessary to determine the relationship between time of egg development in each type site and mean screen temperature, and to use it to estimate incubation periods for the corresponding study areas in 1949. The relationship did not, of course, measure the true association between the variables in each type site. It did, however, provide a measure of the effect of temperature conditions on time of egg development on a relative basis and was satisfactory for practical purposes.

The details of the procedure may now be described as follows:

(1) The median period of development from oviposition to eclosion was determined for each batch of eggs placed in the type sites in 1949 and 1950.

(2) The mean screen temperature associated with each median developmental period was computed.

(3) Median time of development was plotted against mean screen temperature and a smoothed curve of the typical form was obtained for each type site. The approximate median period of egg development could be obtained from the curve for any mean screen temperature.

(4) Egg numbers per unit area were then plotted against time for each study area and a curve was obtained by joining the points by straight lines as in Figure 2. No attempt was made to fit curves as the experimental errors associated with the population counts were fairly high in most cases.

(5) Using the relationship between mean screen temperature and median period of development for the appropriate type site and daily screen temperatures, an estimate of the median developmental period was made for eggs laid the night before count I. This was achieved by a process of adding and averaging the temperatures for successive days after the count until the mean temperature for the time interval gave a period of development equal to the time interval.

(6) The estimated median hatching date so obtained was marked on the time axis of the curve of egg density on time, and the number of eggs present per unit area on that date was read off the curve. This represented the number of eggs laid per unit area during the interval.

(7) The process was repeated, starting with the first estimated median hatching date. It was found that only one or two median hatching dates required estimation in all study areas.

The dominant components of the experimental error associated with the procedure were sampling variance and variance associated with identification when the statistical method of separating mixtures of the species was used. When only *C. gemellata* was present when a count was made, or when the eggs were identified accurately, the variance associated with the estimation of population density was determined in the usual way. When the statistical method of egg identification was used for a population count the sampling variance of *C. gemellata* eggs was computed as:

p^2(sampling variance of x) + $p(1-p)x$, where p was the estimated proportion of *C. gemellata* eggs and x was the population density of the mixture of eggs of both species. To this was added the variance associated with identification (estimated by the formula given in Section II), giving the total variance of the estimate for the particular count date.

Having determined the variances associated with the population counts it was then necessary to compute the variances of the estimates obtained by interpolation from the population curves, i.e. the estimates made between population counts. The variance of each interpolation was estimated as

$$\frac{b^2 \text{ variance } A + a^2 \text{ variance } B}{(a+b)^2},$$

where A and B were the estimates of population density made on two successive count dates, a was the period between the first count date and the point of interpolation on the population curve (c), and b was the period between (c) and the second count date. Departure from linearity was ignored.

The variance of the estimated total seasonal egg production in a study area was the sum of the variances computed for the first population count and the variances of subsequent estimates obtained by interpolation. The results of the estimations are given in Table 8 of the paper.

(ii) *C. hyperici*.—The estimation of the total egg numbers of *C. hyperici* was a much simpler matter because hatching began either shortly before or some time after laying had ceased. For all treeless study areas and some timbered sites the total egg production per unit area was estimated as the total number of individuals per unit area occurring on the date of the mid July count, by which time a few young larvae were present in most areas and oviposition had ceased. The times taken by eggs of this species to complete development in the type sites indicated that few eggs could have hatched before the July count and any larval mortality occurring before then was ignored. The total numbers per unit area in July proved to be an underestimate of the total egg production for another reason. As discussed in Section IX some eggs fell from the plants and were missed. The proportions lost in this way by the end of July appeared to be similar for all study areas (approx. 10 per cent.). Consequently the estimates obtained were satisfactory for practical purposes and could be used with or without an appropriate correction as desired.

In two of the timbered study areas laying ceased by the end of May. For these the total egg production per unit area was estimated as the total number of eggs per unit area recorded late in May (see Table 8, sites 1*c* and 3*c*, 1949). At this time of year egg losses due to dislodgment were negligible and therefore a correction was unnecessary.

The experimental error associated with an estimate was determined in the usual way if the statistical method of egg identification was not used. Where it was employed, the sampling error of the *C. hyperici* eggs was estimated as: $q^2(\text{sampling variance } x) + q(1-q)x$, where q was the estimated proportion of *C. hyperici* eggs and x was the population density of the mixture of eggs of both species. The total variance of the estimate was obtained by adding this to the variance associated with identification and the sampling variance of larval population density. Table 8 gives the estimates uncorrected for loss of eggs from the plants.

(*b*) *In* 1950

The third procedure for estimating total egg production was used for both insects in 1950. It was used for *C. hyperici* in preference to the simpler method described above because oviposition began earlier under considerably warmer conditions, and it was anticipated that a substantial proportion of the eggs would hatch before the July count. This proved to be the case. The statistical method of identification was abandoned completely and the eggs from all samples were kept in the laboratory until they had hatched and could therefore be identified accurately.

The approximate number of eggs of either species laid between two successive population counts in a study area was determined in the following way:

(1) On the date of the first count a large random sample of eggs of each species was collected from immediately around the study area and placed in the corresponding type site. The proportion of fertile eggs (p) (of the species concerned) that had still to complete development in the type site by the time of the second count in the study area was determined. Assuming binomial variation, the standard error of the proportion was estimated as

$$\sqrt{\frac{p(1-p)}{n}},$$

where n was the number of eggs in the sample.

(2) On the assumption that the proportion of unhatched eggs in the study area was similar to that in the type site, the number of residual eggs from count 1 present at count 2 was estimated as px_1 where x_1 was the number of eggs per unit area on the date of count I. The associated variance was estimated as

$$\left(\sqrt{\frac{p(1-p)}{n}}\,x_1\right)^2. \quad \ldots\ \ldots\ \ldots\ \ldots \quad (\mathbf{3})$$

(3) If x_2 was the total number of eggs per unit area present at count 2, then $x_2 - px_1$ was the number of eggs laid during the interval between the counts. Assuming random distributions, the variance due to spatial distribution of these new eggs was estimated as

$$q^2(\text{variance}\ x_2) + q(1-q)x_2, \quad \ldots\ \ldots \quad (\mathbf{4})$$

where q was the estimated proportion of new eggs in x_2.

(4) Then the total variance of the estimate was (**3**) + (**4**).

The total number of eggs laid per unit area was obtained by repetition of the above process and adding the estimates obtained to the number present on the date of the first count. The variance of the total egg production was obtained by summing the variances of the separate estimates. The results are shown in Table 8, the figures for *C. hyperici* being uncorrected for egg dislodgment from the plants. The lower standard errors for the 1950 estimates were due partly to the use of double the 1949 number of sample quadrats.

AN ANALYSIS OF THE OUTBREAKS OF THE AUSTRALIAN PLAGUE LOCUST, *CHORTOICETES TERMINIFERA* (WALKER), DURING THE SEASONS 1940-41 TO 1944-45

By L. R. Clark*

[*Manuscript received March* 11, 1952]

Summary

Outbreaks of the Australian plague locust, *Chortoicetes terminifera* (Walker), occurred each locust season from 1940-41 to 1944-45. The largest outbreak, that of 1942-43, was less severe than those recorded in 1937-38, 1938-39, and 1939-40.

Consideration of the course of these recent outbreaks in relation to temperature and moisture has again demonstrated the importance of these factors as determinants of the regional and seasonal occurrence of swarms. The curve of limiting conditions for the persistence of swarm populations, obtained by Key (1942), was a useful guide for the interpretation of events in the present analysis. However, a number of discrepancies occurred. These were due probably to a variety of causes, e.g. the kind of infestation concerned, the crudeness of the monthly Meyer ratio as an index of soil moisture and pasture conditions, and regional differences in the upper moisture limits at high temperatures. The results of the present investigation suggest that:

(*a*) The limiting Meyer ratios for the persistence or development of a spring infestation of small, weakly gregarious swarms at temperatures between 60 and 70°F. exceed 4-5; either when the September Meyer ratio is 5 or less, or when the spring is preceded by a severe winter drought.

(*b*) At temperatures around 75°F., the maximum Meyer ratio at which swarms can exist is approximately 20.

(*c*) At temperatures near the estimated hatching threshold of 57.5°F., swarm hatchings can occur at Meyer ratios as low as 4-5.

The collapse of the 1942-43 outbreak in part of the main area infested was due apparently to parasitism by an unidentified fly. Similarly, a biotic factor, possibly the same parasite, was largely responsible for the decline of the 1943-44 outbreak during the late spring and early summer.

I. INTRODUCTION

Analyses of outbreaks of the Australian plague locust, *Chortoicetes terminifera* (Walker), have been made by Key (1942, 1943). The work has been continued by the present author with the object of obtaining additional information on the factors controlling outbreaks and checking previous major conclusions. This paper deals with the outbreaks between September 1940 and November 1944.

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II. PROCEDURE

As for Key's analyses, the locust data were provided by the New South Wales and Queensland Locust Information Services developed by C.S.I.R.O. (then C.S.I.R.) with the cooperation of the New South Wales Department of Agriculture and the Queensland Department of Agriculture and Stock. They were described in detail by Key (1942, 1943), the outbreak areas mentioned herein (Table 1) described in the same author's 1945 paper. Meteorological data were supplied by the Commonwealth Bureau of Meteorology.

The monthly maps containing locust data from Pastures Protection (P.P.) and Stock Districts were combined to form monthly composite maps. The locust data from the composite maps were transferred to smaller maps and correlation made between the areas infested monthly and climatic factors by drawing isopleths for different values of the factors concerned. Detailed examinations of the data for particular regions, involving consideration of rainfall distribution etc., were made when necessary.

TABLE 1

KEY TO TOWNS SHOWN IN THE MAPS

AE	Armidale	CS	Cairns	LH	Longreach	PS	Parkes
AY	Albury	CT	Charters Towers	LN	Leeton	QI	Quirindi
BA	Bingara	CU	Curban	LT	Lockhart	RA	Roma
BE	Bourke	CW	Camooweal	MA	Manilla	RN	Rockhampton
BG	Bundaberg	CY	Cloncurry	ME	Moree	SN	Singleton
BH	Broken Hill	DN	Deniliquin	MH	Maryborough	TD	Thurloo Downs
BI	Brisbane	DO	Dandaloo	MI	Murrurundi	TE	Trangie
BL	Blackall	DU	Dubbo	ML	Mitchell	TH	Tamworth
BR	Barcaldine	EA	Eromanga	MN	Merrygoen	TL	Tocumwal
BT	Bathurst	ED	Emerald	MP	Mount Hope	TO	Townsville
BU	Boulia	FS	Forbes	MU	Mudgee	WE	Wentworth
BY	Binnaway	GA	Gilgandra	MW	Mulwala	WG	Wyalong
CA	Canberra	GH	Griffith	MY	Mackay	WH	Windorah
CB	Coonamble	GI	Glen Innes	NA	Narrandera	WK	Warwick
CE	Clermont	GN	Goulburn	NE	Narromine	WL	Wellington
CH	Chinchilla	GU	Gunnedah	NI	Narrabri	WN	Warren
CI	Collarenebri	HN	Hillston	NN	Normanton	WT	Walgett
CN	Coonabarabran	HU	Hughenden	OE	Orange	WW	Wagga Wagga
CO	Cobar	IL	Inverell	PH	Peak Hill	YG	Young
CR	Corowa						

The mean monthly air temperature was used as the measure of temperature. The monthly Meyer ratio (Precipitation/Saturation deficit) was used as the index to moisture conditions. To obtain Meyer ratios for weather stations that did not record humidity, it was necessary to estimate the saturation deficit by drawing isopleths based on stations recording temperature and humidity and interpolating between them, appropriate allowances being made for altitude.

III. Description and Analysis of Outbreaks

(a) *The Outbreak of* 1940-41

(i) *Description.*—The first swarm record for the 1940-41 season was received from the Armidale P.P. District (N.S.W.). This hatching occurred late in August north-east of Bundarra. It is most unlikely that the acridid concerned was *Chortoicetes,* hatchings of which were not reported elsewhere until late the following month. It is probable that the species was *Austroicetes cruciata* (Sauss.). This grasshopper was numerous in many parts of New South Wales during the spring of 1940-41, and normally hatches approximately a month before *Chortoicetes.*

Table 2

DETAILS OF THE 1940-41 OUTBREAK

Month	Total Swarms Reported	Total Area (sq. miles) From Which Swarms Were Reported
September	67	23,500
October	92	4,900
November	26	3,250
December	0	0

During the following month swarm hatchings appeared over a considerable area (Fig. 1). In all, 61 swarms were reported from New South Wales and six from Queensland (Table 2). All records from New South Wales were for young hoppers, showing that general hatching began during the month. All the hopper bands present in this State were described as small, loose swarms. In addition to swarm hatchings, non-swarming populations of high density appeared throughout an extensive area between Moree and Parkes adjacent to that in which swarm hatchings were observed.

In Queensland, one band of old hoppers was seen near Charters Towers in an area free from swarms during the 1939-40 season. The identity of the species concerned could not be established. Light infestations of young *Chortoicetes* hoppers occurred around Oakey and Warwick. The area infested around Warwick was continuous with that in New South Wales. A single flying swarm, probably *Chortoicetes,* was seen near Julia Creek, due south of Millungra.

The infested area, which began to shrink before the end of September, decreased again during October (Figs. 1 and 2). There was a corresponding increase in the area occupied by non-swarming populations of high density. A few small hopper bands were seen near Trangie and Tullamore (N.S.W.). For this area it is difficult to form a reliable estimate of the *Chortoicetes* infestation as *Austroicetes cruciata* was numerous. It is probable that the hopper bands referred to were *Chortoicetes* because most individuals of the other species would have reached the flying stage before the observation was made.

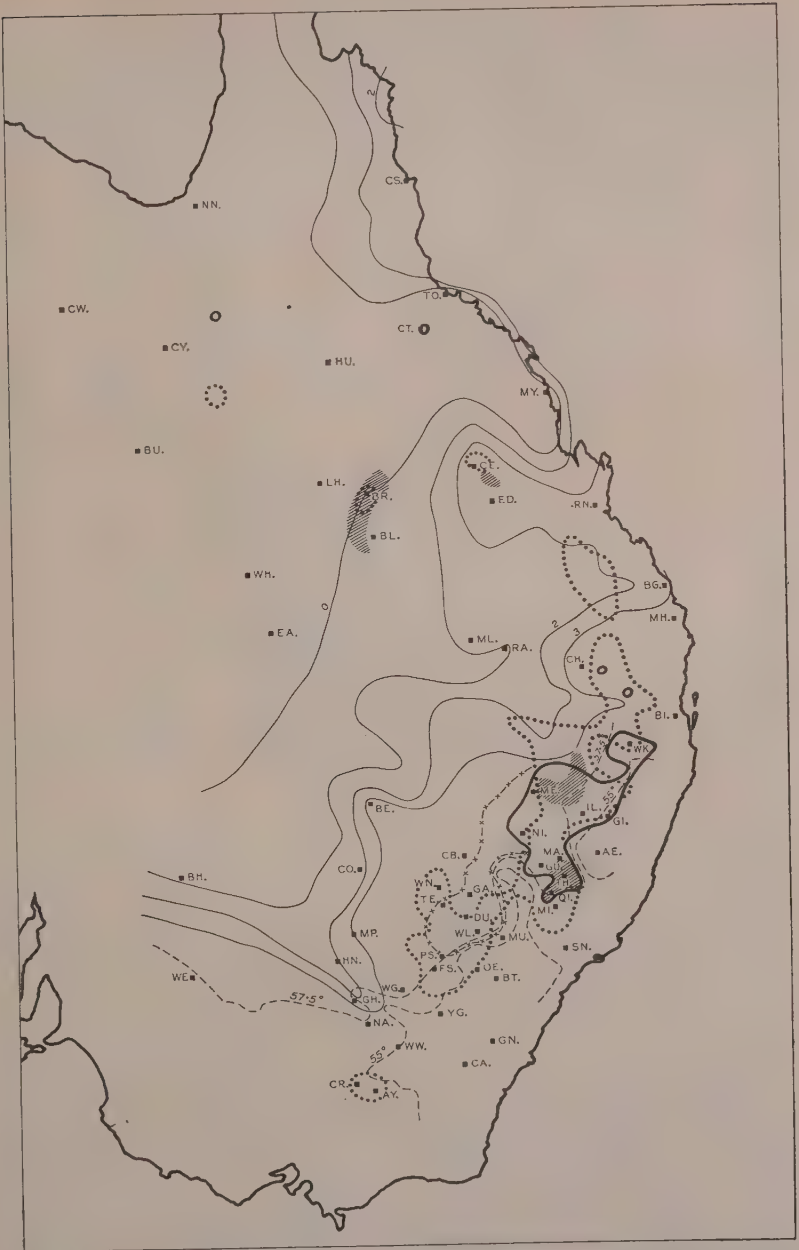

Fig. 1.—Areas infested by swarms in September 1940, ——. Limits of second-generation swarms, 1939-40 season (after Key 1943), ... Shaded areas—limits of third-generation swarms, 1939-40 season (after Key 1943). Western limit of area adjoining area infested by swarms in September 1940 in which non-swarming populations of high density were recorded, —×—×— . Isotherms for 57.5 and 55°F., - - - - . Isopleths for Meyer ratios of 0, 1, 2, and 3, ——— .

From New South Wales 90 records of swarms were received for October. The increase in swarm numbers was due to early October hatchings. In Queensland swarms were limited to two small areas. A small infestation of hoppers occurred near Eidsvold, and flying locusts were seen near Jandowae. The available evidence suggests that these adults had overwintered from the previous season.

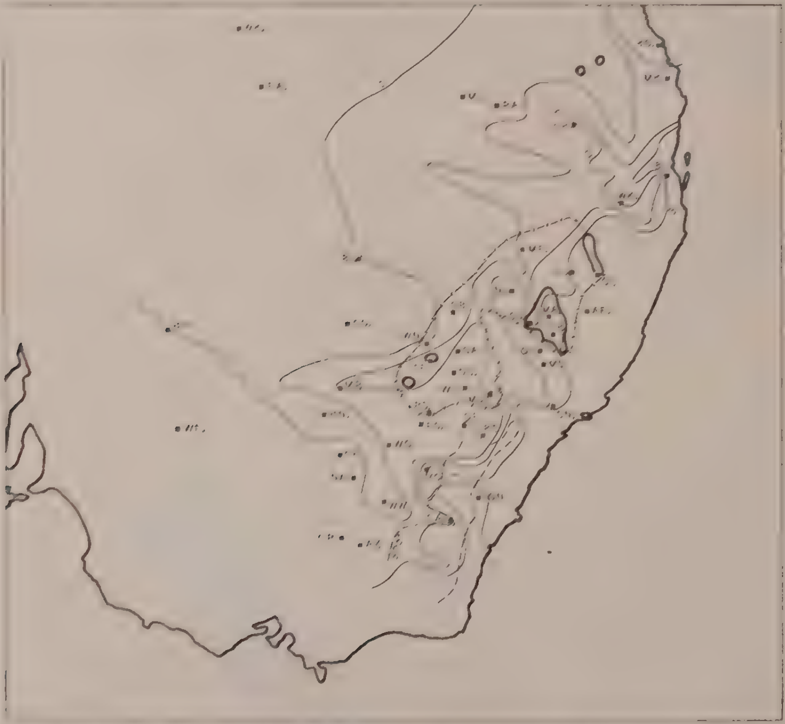

Fig. 2.—Limits of areas infested by swarms in October 1940, ——— . Limits of area containing non-swarming populations of high density, — / — / — . Isopleths for Meyer ratio, ———. Isotherm for 57.5°F., - - - - .

In November hopper bands were present in the area surrounded by Barraba, Boggabri, Gunnedah, Tamworth, and Manilla (Fig. 3), but they disintegrated before the end of the month. No flying swarms were reported, showing that population numbers fell below the level at which swarm coherence can be maintained before the adult stage was reached. The area occupied by non-swarming populations of high density was greatly reduced by the end of October, and in November was limited to places around Glen Innes and Cassilis (N.S.W.). No further reports of swarms were received for the season.

In April 1941 non-swarming populations of high density were observed east of Pilliga and between Trangie and Dandaloo (N.S.W.). These are the only records that referred definitely to *Chortoicetes*, and show that locust numbers were increasing again in the Bogan-Macquarie and MacIntyre-Gwydir outbreak areas.

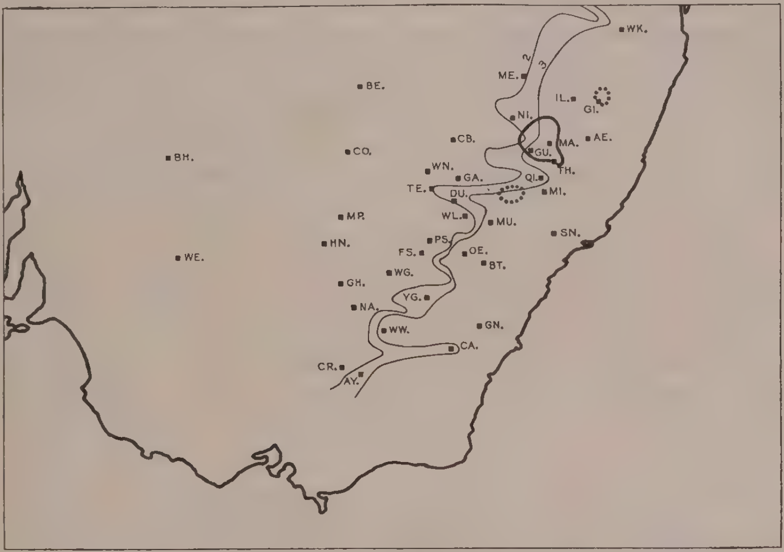

Fig. 3.—Limits of area infested by swarms in November 1940, ——— . Limits of areas containing non-swarming populations of high density, ... Isopleths for Meyer ratio, ——— .

(ii) *Analysis.*—Before considering the influence of weather conditions on the outbreak of 1940-41, it must be related to the infestation of 1939-40 to establish the origin of the swarms. Key's (1943) description of the 1939-40 outbreak shows that the swarm locusts hatched during the spring of 1940-41 were probably all the progeny of swarms, mainly of the second generation of the previous season. The facts that the hatchings of 1940-41 were only of small, loose swarms and that the total number was lower than during the previous late summer and autumn indicate that substantial egg or hopper mortalities occurred before the season began.

The areas containing swarms in September 1940 are shown in Figure 1. Isopleths for monthly Meyer ratios of 0, 1, 2, and 3, together with isotherms for 55 and 57.5°F., have been included to indicate the associated weather conditions. Key (1942) obtained a curve of limiting conditions for the completion of egg development and hatching of swarms by plotting the air temperatures and Meyer ratios prevailing on the hatching dates of swarms for several generations. The points for hatching were grouped into Meyer ratio classes of two units and the mean temperature for each group was plotted against the mean Meyer ratio. The curve is reproduced in Figure 4. The minimum hatching temperature shown is 57.5°F., the corresponding Meyer ratio being 11-12.

In Queensland, this threshold temperature was exceeded by the monthly mean in the places where swarms hatched in September. In New South Wales, as shown in Figure 1, the isotherm for 57.5°F. passes through the main infested area. That for 55°F. also passes into the area close to its eastern border. On the "cold" side of the isotherm for 57.5°F. general hatching began, on an average, 1-2 weeks later than on the "warm" side in places experiencing similar moisture conditions.

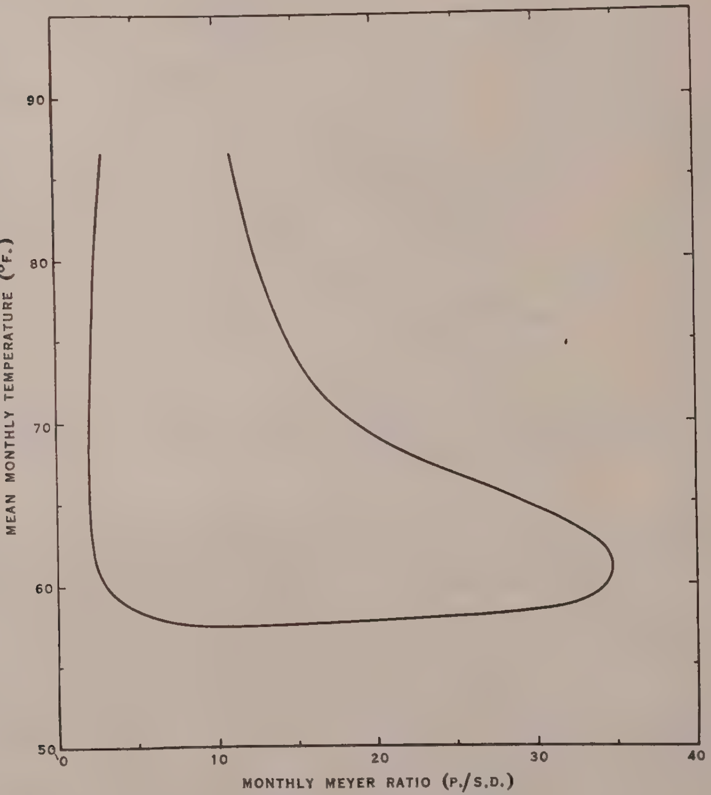

Fig. 4.—Curve of limiting conditions for the persistence of an infestation of swarms in the field. (After Key 1942.)

To obtain an estimate of the lowest temperatures at which swarm hatching began, conditions were examined for the two weather stations (Warialda and Tenterfield) around which hatchings occurred on the cold side of the isotherm for 57.5°F. Bioclimatographs were constructed to show the observed hatching dates of the first swarms and the temperatures at hatching. These were 56 and

57.5°F., remarkably close to the hatching threshold estimated by Key. However, the Meyer ratios associated with these temperatures were between 4 and 5 — lower than both the average value obtained by Key and the individual determinations on which it was based.

Concerning his curve, Key concluded that "for most of its length, at least, the curve also represents approximately the vital limits for the active stages, and thus the limits for the completion of the life cycle." The curve was derived from a study of swarming populations only and, strictly, represents average values for the temperature-moisture limits at which swarms can persist. At temperatures similar to those occurring in the area infested in October and early November 1940 (between 60 and 70°F.) the curve shows a minimum moisture limit of approximately 2. When considering the course of the 1940-41 outbreak in relation to Key's limits, the following points are relevant:

(1) In September the area infested in New South Wales lay on the "wet" side of the isopleth for a Meyer ratio of 3. Within the area the monthly Meyer ratios ranged from 3.6 to 11.2, the mean being 5.5. This value is close to the estimated moisture limits at which swarms can persist at the temperatures recorded (58-60°F.). Part of the Queensland infestation occurred in the zone of zero Meyer ratio and the remainder in the same moisture zone as that in New South Wales.

(2) The map for October and the individual locust reports showed that the principal infested area diminished during September and broke into two parts. In these the Meyer ratios exceeded 2 except in one small section, and were around 4 for half of the remainder.

(3) Although the monthly Meyer ratio exceeded 2 in practically all of the area infested in November (range in Meyer ratio 1.7-6.9), the remaining swarms disappeared before the adult stage was reached.

It may be assumed that the decline of this outbreak was not caused by biotic factors such as parasitism, or by control work. The field observers, who were still able to operate efficiently at this early stage of the World War, found no signs of parasitism or disease; and scarcely any control work was attempted. The available evidence indicates that the disintegration of hopper bands throughout the entire area followed mortality caused by unfavourably dry conditions — although Meyer ratios favourable in regard to rainfall distribution and Key's limits occurred each month in part of the area infested.

Unlike the swarms studied by Key, which, for the most part, were large, dense, and strongly gregarious, those involved in the present analysis were small and of low density. The writer has observed that, even when the mortality rate is only moderately high, such swarms disintegrate rapidly; whereas swarms initially much larger and denser are frequently able to maintain coherence after suffering a similar percentage reduction in locust numbers. It follows that the lower moisture limits for the continued existence of small, loose swarms would frequently be higher than those at which coherence can be maintained by large, dense swarms. The collapse of the 1940-41 outbreak suggests that Meyer ratios considerably higher than 4 would be necessary for the persistence of an infestation of the type described in October and November.

Of considerable interest is the fact that nearly all the hopper bands that hatched in September disintegrated before the end of the month. A few bands maintained coherence in areas in which the September Meyer ratio exceeded 6. Even where the highest Meyer ratios (8.9-11.2) occurred, the local observers reported the disappearance of hopper bands, and attributed the mortality to "lack of green feed." The amount of green feed available to hoppers in September was unusually small. Owing to the severe winter drought of 1940 (see Table 3), stock had grazed most pastures practically to ground level before hatching by *Chortoicetes* began. The light-moderate September rains had little or no effect on the condition of the heavily overgrazed pastures. Had the winter rainfall been considerably higher, it is probable that many more hopper bands would have maintained coherence in October.*

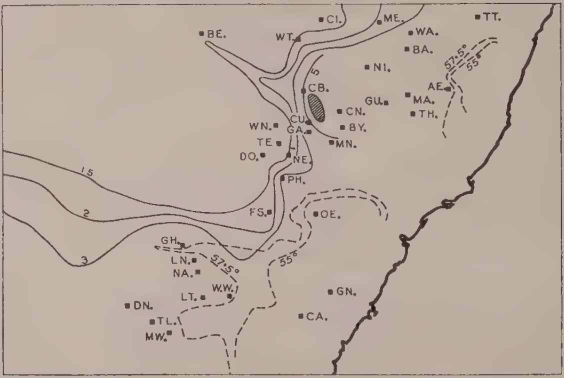

Fig. 5.—Limits of the New South Wales area infested by swarms in October 1941 (area hatched). Other symbols as in earlier figures.

The shortage of green feed and "shelter" vegetation (Clark 1947) continued after September, and almost certainly caused most of the hopper mortality occurring in October and November. The rainfall for these months was not sufficient to change the situation in favour of *Chortoicetes,* even in areas where Meyer ratios around 10 were recorded in September. It is concluded that Meyer ratios much higher than Key's lower limits would be necessary for the persistence of an infestation of small, weakly gregarious swarms during October and November after a severe winter drought.

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* In September 1939, small hopper bands hatched in the Trangie-Gilgandra area at a Meyer ratio of approximately 2 (temperature 56°F.), and managed to preserve swarm formation into October (see Key 1943, p. 28, Figure 7). The winter of 1939 was much wetter than that of 1940. In the Trangie area, where the writer was stationed, 3 in. of rain fell in August and plenty of green feed was available to *Chortoicetes* after hatching.

(*b*) *The Outbreak of* 1941-42

(i) *Description.*—The 1941-42 outbreak of *Chortoicetes* was the least severe for several years, and only a small part of New South Wales was affected. The first hopper bands were observed in October, although general hatching began late in September. Five hopper bands of low density were noted by an official observer south-east of Coonamble (Fig. 5). A road survey made by the writer in October showed that the infestation was at first a little more extensive on the western side than indicated in the figure which, as usual, is based on data received from the local observer. Non-swarming populations of high density were reported around Trangie, another part of the Bogan-Macquarie outbreak area. *Chortoicetes* was also present in similar numbers in parts of the Warialda P.P. District, just east of Inverell, and north of Molong.

In November (Fig. 6), three flying swarms were reported from the western part of the Coonabarabran P.P. District, in a narrow strip of country lying between the Bogan-Macquarie and Warrumbungles outbreak areas. The following month no report was received from the local observer. It can be assumed that the flying swarms present late in November persisted into early December. However, a high mortality probably occurred later in the month when locust numbers decreased greatly in nearby parts of the Bogan-Macquarie outbreak area.

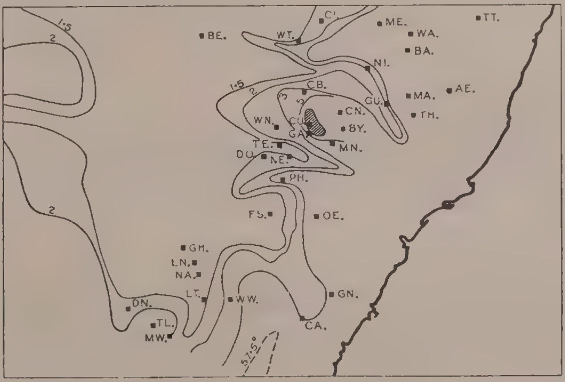

Fig. 6.—Limits of the New South Wales area infested by swarms in November 1941 (area hatched). Other symbols as before.

Several small flying swarms were observed in December south of Mathoura, near the Murray River. These hatched east of Tocumwal in the Walliston area and laid in the Wamboota district. A few small swarms were also reported from Lockhart, Mulwala, and Tocumwal. Key (1945) mentioned these swarms and discussed the fact that their development from non-swarming populations was evidence of the existence of outbreak area country additional to his suspected "south-western" outbreak area, and consequently extended it to form his

TABLE 3

MONTHLY RAINFALLS (POINTS) AND CORRESPONDING MONTHLY MEANS (IN BRACKETS) FOR STATIONS IN THE AREA INFESTED FOR THE PERIOD APRIL-NOVEMBER 1940

Station	April	May	June	July	August	September	October	November
Warwick	7(164)	97(154)	64(180)	0(182)	7(151)	122(180)	94(229)	435(255)
Killarney	20(190)	75(147)	52(201)	0(184)	6(132)	0(176)	0(221)	0(263)
Stanthorpe	20(172)	55(185)	103(196)	13(203)	17(182)	109(228)	117(255)	220(269)
Tenterfield	49(178)	60(172)	69(227)	27(226)	36(178)	101(211)	162(267)	198(314)
Warialda	121(173)	14(175)	17(221)	9(176)	42(172)	96(179)	86(212)	181(242)
Inverell	98(189)	32(191)	34(238)	0(202)	83(187)	82(196)	112(255)	239(273)
Gunnedah	187(156)	0(156)	136(191)	3(157)	83(181)	135(157)	58(188)	156(207)
Glen Innes	146(163)	30(166)	75(247)	17(196)	46(192)	106(194)	136(293)	126(300)
Bundarra	112(201)	41(157)	59(240)	2(177)	52(192)	145(195)	103(266)	256(286)
Bingara	144(186)	33(222)	43(233)	6(185)	83(206)	120(200)	98(271)	149(297)
Manilla	170(189)	12(161)	58(203)	3(145)	78(154)	178(169)	132(213)	202(253)
Tamworth	? (180)	? (160)	48(232)	58(181)	23(181)	224(202)	100(214)	277(270)
Moree	79(140)	45(161)	64(199)	5(194)	39(129)	119(138)	62(185)	92(200)
Narrabri	180(171)	32(186)	39(239)	0(184)	91(159)	123(158)	119(182)	113(225)
Quirindi	207(179)	22(170)	29(246)	20(187)	113(187)	130(177)	77(214)	111(251)

"Riverina" outbreak area. Further discussion is unnecessary here except to say that the present author is in agreement with Key's conclusion on the basis of this evidence and data obtained during previous outbreaks. Non-swarming populations of high density were reported this month from east of Cowra and north of Molong.

No reports of swarms were received in January 1942. In February, general hatching occurred in the Coonabarabran P.P. District early in the month, and two small, dense bands of young hoppers were reported 2-3 weeks later. No swarms were seen during March but non-swarming populations of high density were reported from the Tamworth P.P. District.

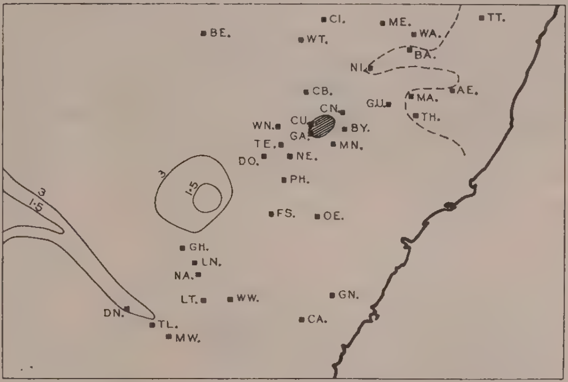

Fig. 7.—Limits of the New South Wales area infested by swarms in February 1942 (area hatched). Isopleths for Meyer ratio—. Western limit of area in which conditions must have been unfavourably moist for *Chortoicetes* in terms of Key's (1942) curve of limiting conditions, - - - .

In April an extensive area in the southern part of the Coonabarabran P.P. District was infested by an unspecified number of flying swarms of low density (Fig. 8). This area was approximately three times the size of that infested earlier in the season. These swarms disintegrated before the end of the month. Two isolated flying swarms were seen in the Wanaaring P.P. District, which is situated in the north-western corner of the State.

(ii) *Analysis.*—The outbreak of *Chortoicetes* during the 1940-41 locust season ended in November. Following the heavy rains of January 1941, population numbers began to increase again in the Bogan-Macquarie, MacIntyre-Gwydir, and Warrumbungles outbreak areas. Thus the first conclusion of importance is that the swarms observed during the spring of 1941-42 were not the progeny of previous swarms, but resulted from the multiplication of non-swarming populations in outbreak area country.

In the parts of the Coonabarabran P.P. District in which the infestation developed, the population densities of *Chortoicetes* in active outbreak centres must have been close to the minimum at which swarm formation is possible. Observations made in this area and nearby parts of the Bogan-Macquarie outbreak area suggest that the process of real concentration (i.e. concentration by active centripetal movements (see Kennedy 1939, p. 406)) played an unusually important role in swarm development. During the late summer and early autumn of 1940-41 the mean adult population densities following movement into the food-shelter habitat of some outbreak centres between Trangie and Gilgandra rose from about 0.25 to 0.75 per sq. yd. Following concentrated laying in the adjacent oviposition habitat by the females of such populations, hopper hatching densities up to 20-30 per sq. yd. occurred the following spring. After the pasture vegetation began to dry out the hoppers accumulated on the remaining patches of green feed, first in the oviposition habitat and then in the food-shelter nuclei of the food-shelter habitat (see Key 1945 or Clark 1947 for definitions). These active concentrations resulted in densities as high as 100 per sq. yd. By the time the fifth instar was reached many of the densest populations of hoppers were exhibiting incipient swarm formation.

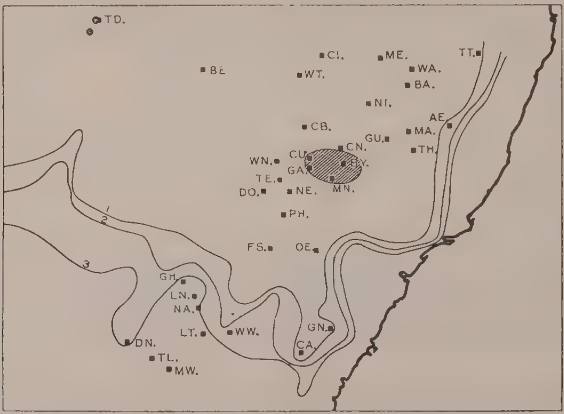

Fig. 8.—Limits of the New South Wales area infested by swarms in April 1942 (area hatched) and isopleths for Meyer ratio.

From Figure 5 it is apparent that the area in which hopper swarms developed in October 1941 lies just on the wet side of the isopleth for a Meyer ratio of 5. On the dry side of this isopleth similar hatching populations further west in the Bogan-Macquarie outbreak area failed to produce swarms under similar temperature conditions (around 63°F.) because of high mortality late in the hopper stage. Field studies indicate that this mortality was due principally to a shortage of green feed. Parasites and predators were much too scarce to have played a significant role, and no diseased locusts were found. Thus it appears that moisture was the decisive factor, and that Meyer ratios of 5 or more were necessary for swarm development in the first stages of this outbreak.

This conclusion agrees with the suggestion made in Section III (*a*) (ii), that Meyer ratios exceeding 4 are necessary for the persistence of a spring infestation of small, loose swarms.

In the area in which the incipient outbreak collapsed in 1941, the winter rainfall was much higher than that for the principal area infested in 1940, and much more green feed was present when general hatching began late in September. However, the Meyer ratios for this month were only 4-5. Had they been much higher more green feed would have been available to hoppers in October, and some swarms might have developed. Thus, as in 1940, we have an instance in which the limiting moisture conditions in October were probably influenced by the preceding rainfall.

As shown in Figure 6, swarms maintained coherence into November. The mean monthly Meyer ratio for the area was again approximately 6. These swarms of adults disintegrated some time during December, when conditions were very dry (Meyer ratio 1). Although most eggs were laid in late November and early December, general hatching of the second generation did not begin until early in February, approximately 2 months later.

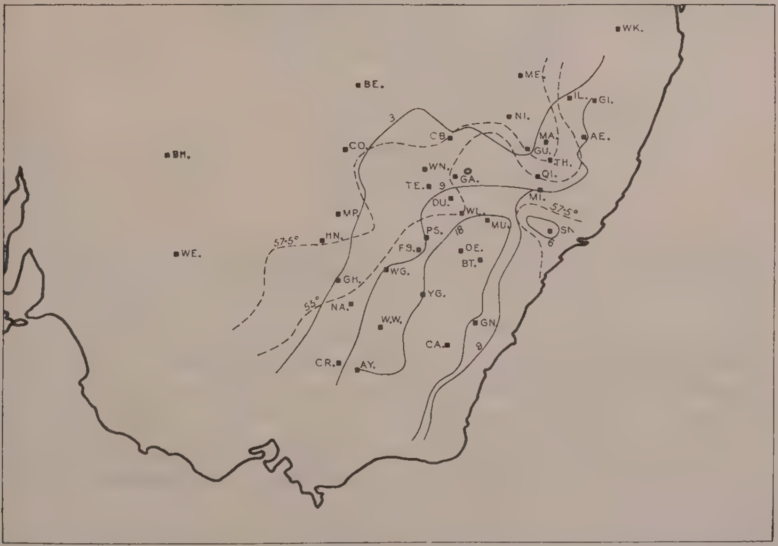

Fig. 9.—Limits of the New South Wales area infested by swarms in September 1942 (——), together with isopleths for Meyer ratio (——) and isotherms for 55 and 57.5°F. (– – – –).

According to Key (1942), egg development to hatching is normally completed in 2½ weeks at this time of year, providing soil moisture conditions are favourable. Conditions in December were undoubtedly too dry for unretarded egg development, but the mean Meyer ratio for the infested area in January was approximately 4. At this value egg development should proceed rapidly to eclosion at temperatures over 70°F. An examination of the rainfall data for the five weather stations in the area showed that the only rain recorded fell on January 15 and 16. Thus the Meyer ratio of approximately 4, with a correction for saturation deficit, applies only to the second half of the month. Hatching began 2½-3 weeks after the January rains, a period similar to the average for complete development under favourable conditions. It appears that eggs of *Chortoicetes* can survive at least 6 weeks of drought without high mortality (see also Key 1942, p. 54).

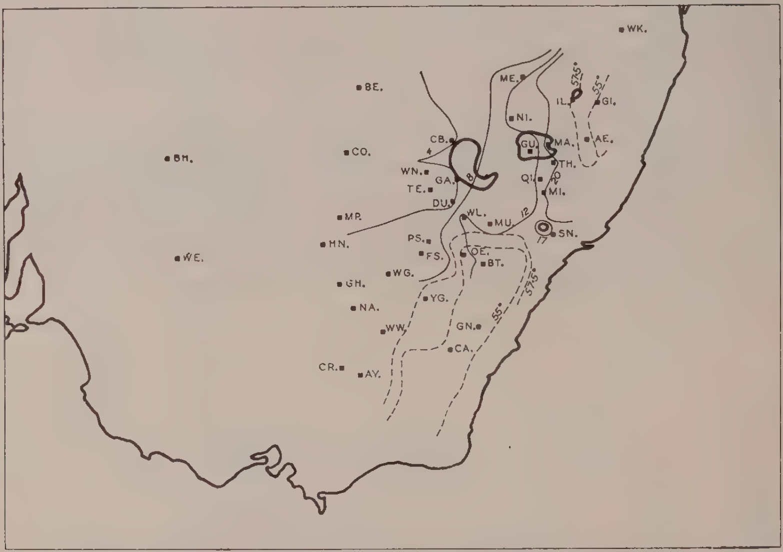

Fig. 10.—Limits of the New South Wales areas infested by swarms in October 1942 (——), isopleths for Meyer ratio (——), and isotherms for 55 and 57.5°F. (– – – –).

February was a favourable month and the outbreak continued (Fig. 7). The mean monthly Meyer ratio for stations in the area was 5.5. In March the mean monthly Meyer ratio was 5.2. No swarms were observed, but it can be assumed that some were present because flying swarms were reported the following month, when an increase was recorded in the size of the area infested (Fig. 8). No rain fell during April and the swarms disintegrated before the end of the month. Thus dry conditions hastened the end of the outbreak before the onset of winter.

Population data were too few for a satisfactory analysis of the occurrence of isolated swarms in the Riverina outbreak area. These swarms were not reported until December. Apparently conditions were too dry for swarms of the second generation to develop.

No data are available to determine the origin of the two flying swarms observed in the north-western corner of New South Wales in April.

(*c*) *The Outbreak of* 1942-43

(i) *Description*.—The first records of swarm hatching were received in September 1942. Towards the end of this month three swarms of young hoppers were observed between Gilgandra and Tooraweenah (Fig. 9). In October extensive hatchings of swarms were reported from parts of New South Wales, namely just north of Inverell, Jerry's Plains, near Cassilis, in adjacent parts of the Coonamble, Coonabarabran, and Dubbo P.P. Districts, and in the Liverpool Plains. The infestation was heaviest in the Coonabarabran district and Liverpool Plains. The first flying swarms of the season appeared in the latter area towards the end of the month (Fig. 10).

During November flying swarms increased in numbers and the total infested area expanded. The swarms near Inverell died out. A new area of infestation was reported, extending from Pokataroo to Moree and Bellata (Fig. 11). The swarms present were all of adults, suggesting that they had been missed the previous month when in the hopper stage. Before the end of the month laying was observed in the two largest areas.

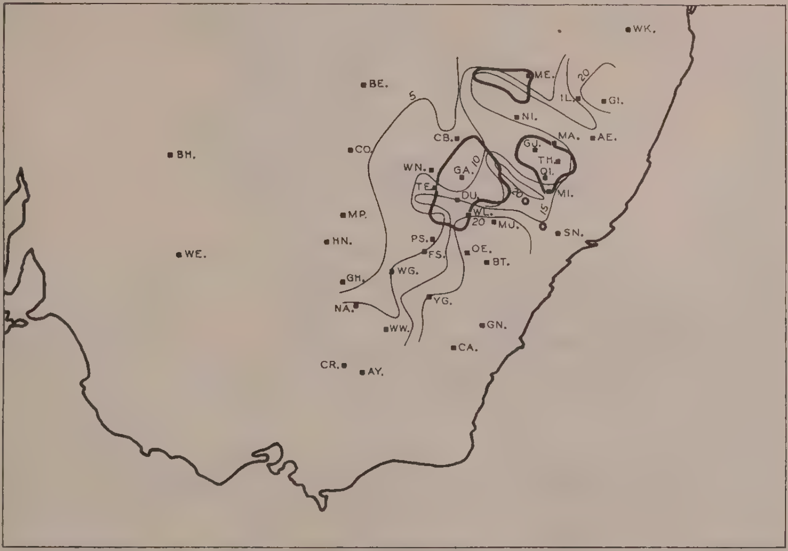

Fig. 11.—Limits of the New South Wales areas infested by swarms in November 1942, together with isopleths for Meyer ratio (symbols as before).

As a result of the migration of flying swarms the three main infested areas joined in December (Fig. 12). Most of the swarms that had originated in and near the Coonabarabran District disappeared by the end of the month, as did those hatched in the Liverpool Plains. In both areas laying continued in December. Some of the swarms that had originated north of Narrabri also laid during the month. The infestation in the Hunter River valley extended as a result of migration. Swarms of the second generation hatched during the month both there and in the main area infested in New South Wales. In Queensland the first swarms of the season were reported from around Hughenden.

In New South Wales the second generation continued to hatch during January (Fig. 13), particularly between Moree and Narrabri, Boggabri, Tamworth, and Quirindi. Some flying swarms were reported, most of which were of the second generation. A new infestation of flying swarms was reported in the vicinity of Walgett and Carinda. These swarms may have moved unnoticed down the Barwon River from the Pokataroo area. However, it is more likely that they were of local origin in view of the differences in the dates on which flying swarms were first observed in each area. They were seen near Walgett and Carinda earlier in the month than at Pokataroo.

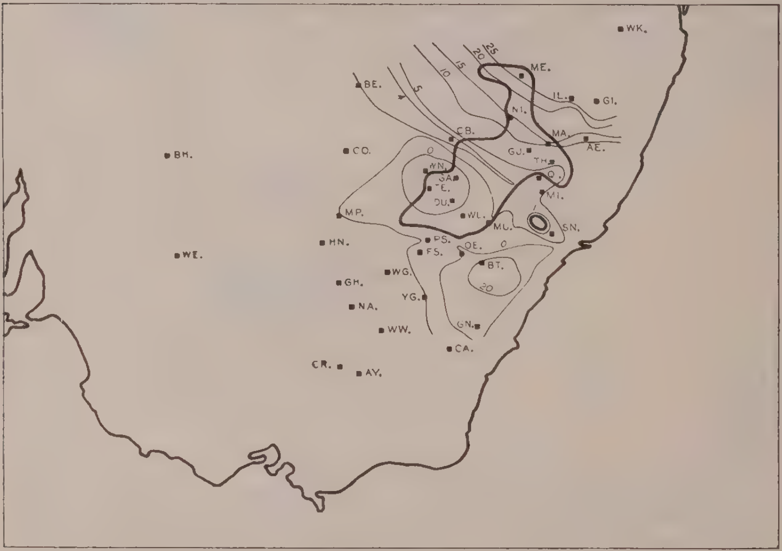

Fig. 12.—Limits of the New South Wales areas infested by swarms in December 1942, together with isopleths for Meyer ratio (symbols as before).

Flying swarms were also observed near Barmedman and Bimbi, south of the main area infested. Reports stated that they arrived from the west and north-west. This suggests that these swarms originated in the Bland outbreak area (see Key 1945, map 3). The reported existence of a swarm-free area between the two infestations is reliable because the districts concerned are closely settled. It is probable that swarms were present in the Hunter River valley, but the field observer's report for this month was indefinite. In Queensland the infestation around Hughenden persisted, and a flying swarm was observed near Julia Creek.

In February the main area infested in New South Wales showed a decrease in the northern part of the State and an extension southwards (Fig. 14). Small infestations persisted around Pokataroo and in the Hunter River valley. The total number of swarms, which had increased up to January, fell considerably in February, suggesting that the outbreak was waning (Table 4). Laying by swarms of the second generation began early in the month, and occurred extensively throughout the areas infested in New South Wales. Young hopper swarms were reported from the main area infested and the Hunter River valley. These were late hatchings of the second generation. Swarms continued to enter the southernmost parts of the main infested area from the west as well as the north. This is further evidence that the Bland outbreak area was active. In Queensland, swarms of old hoppers and adults were again observed around Hughenden. Flying swarms were seen also near Jandowae and Killarney.

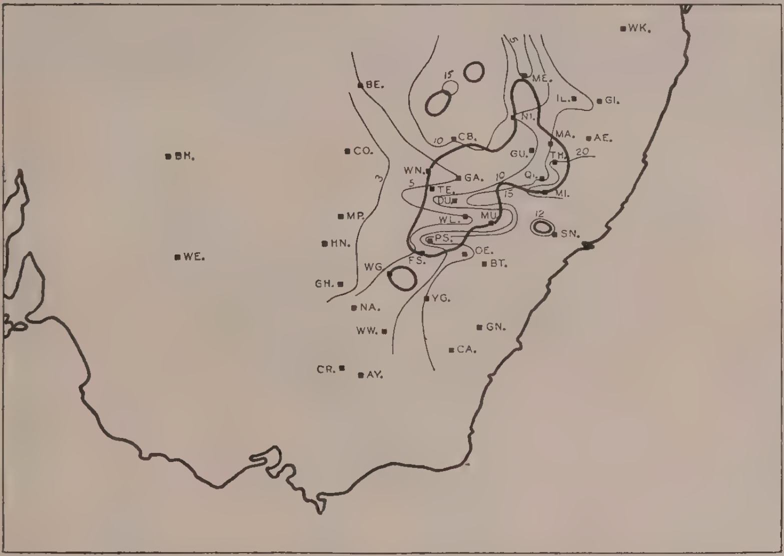

Fig. 13.—Limits of the New South Wales areas infested by swarms in January 1943, together with isopleths for Meyer ratio (symbols as before).

TABLE 4

DETAILS OF THE 1942-43 OUTBREAK

Month	New South Wales		Queensland	
	Total Number of Swarms Reported	Total Area Infested (sq. miles)	Total Number of Swarms Reported	Total Area Infested (sq. miles)
September	4	100	—	—
October	63	4,500	—	—
November	64	16,150	—	—
December	110	25,600	6	2,300
January	140	27,400	7	2,800
February	97	20,800	5	1,600
March	37	8,400	1	100
April	1	50	—	—
May	—	—	1	50

The decrease in the total area infested continued during March. The data for this month (Fig. 15) showed that the main area infested broke up into three parts. Numerous egg beds were reported but no hatchings. Laying continued in all three parts. In the Hunter River valley a few swarms of old hoppers and adults persisted until late in the month. By early April the infestation had died out in all parts of New South Wales except a small area near Quirindi, where a swarm of young hoppers was seen. These were possibly of the third generation.

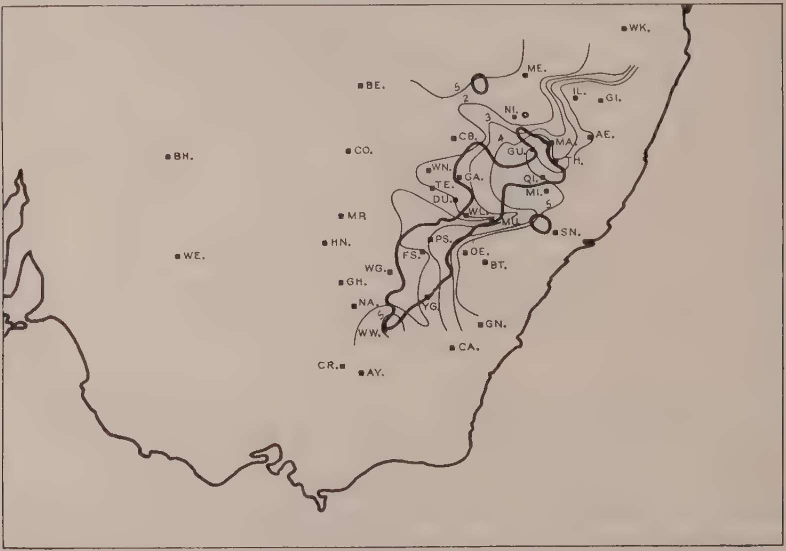

Fig. 14.—Limits of the New South Wales areas infested by swarms in February 1943, together with isopleths for Meyer ratio (symbols as before).

In May no swarms were observed in New South Wales. A single swarm of old hoppers was reported from Queensland in the vicinity of Millmerran. The outbreak is summarized month by month in Table 4. It was more extensive and severe than the minor infestations occurring in 1940-41 and 1941-42, but less so than the 1937-38, 1938-39, and 1939-40 outbreaks.

(ii) *Analysis*.—During the 1941-42 season an infestation of small swarms developed in the Coonabarabran P.P. District (Section (*b*)). Elsewhere only a few isolated swarms were observed, and few reports of non-swarming populations of high density were received. However, an extensive outbreak began in the spring of 1942-43. If one counts a generation as from hatching to hatching, widespread swarming occurred in the fourth generation following the reduction of population numbers to a very low level in the spring of 1940-41. In the Coonabarabran P.P. District locust survival was sufficiently high for swarms to appear in the second generation after the spring of 1940-41.

Most hatching of the spring generation occurred in October (Fig. 10). Conditions during this month were favourable for the maintenance of an infestation except in the Inverell area. The monthly Meyer ratio at Inverell was 52.5, a value greatly exceeding tthe upper favourable moisture limit determined by Key. This infestation was said to have been destroyed by poison baiting and bird predation. However, moisture conditions alone could possibly account for its collapse. The swarms in this area must have resulted from local multiplication, and their formation was used by Key (1945, p. 96) as part of the evidence leading him to recognize the Inverell outbreak area. Similarly, the swarms reported near Cassilis could only have originated in the Coolah district, and supplied the major ground for recognizing the Coolah outbreak area (Key 1945, p. 95).

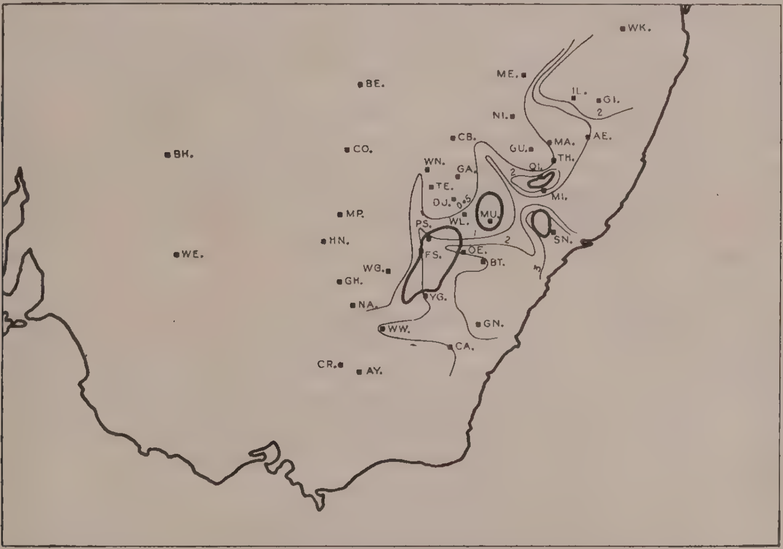

Fig. 15.—Limits of the New South Wales areas infested by swarms in March 1943, together with isopleths for Meyer ratio (symbols as before).

In November (Fig. 11) favourable moisture conditions continued and the major infested areas expanded with adult migration. The new infestation which appeared in the MacIntyre-Gwydir outbreak area could only have resulted from local multiplication. The following month, the only infested area in which very little rain fell was the Hunter River valley. The monthly Meyer ratio was only 1.0, an unfavourably low value in terms of Key's limits. However, the infestation persisted, presumably because of the residual effect of the very moist but favourable conditions occurring during the previous month.

The map for December shows that the main areas infested in New South Wales joined to form a single very large area (Fig. 12). In the extreme north of this area conditions must have been unfavourably moist because most swarms were eliminated by the end of the month (compare Figs. 12 and 13). All the swarms disappeared from the area in which the Meyer ratio exceeded 25, and most from the places where the Meyer ratios ranged between 20 and 25. The infestation continued undiminished in the zone of Meyer ratios ranging from 15 to 20. This suggests that the upper moisture limit for the persistence of an infestation at the prevailing temperatures (74-76°F.) is close to 20. The corresponding upper moisture limit estimated by Key (1942) is approximately 13-14.

A likely explanation of the discrepancy between these results is that the other worker obtained his few data on the upper moisture limits at high temperatures from Queensland areas in which a continuous, very dense pasture growth develops rapidly after heavy summer rains (Key 1945). Very dense herbaceous vegetation is unfavourable to *Chortoicetes*, probably because the associated microclimatic conditions favour the development of fungal diseases. Owing to pasture differences between the region involved in the present analysis and that in Queensland, it is considered that much higher Meyer ratios would be necessary in the former to produce equally unfavourable habitat conditions over extensive areas.

The first swarm records from Queensland were received in December. The outbreak in this State was only a very minor one. It was not suitable for detailed analysis owing to the scarcity of meteorological stations in the areas concerned. As no swarms were observed in Queensland during the previous season, it is concluded that those reported in 1942-43 resulted from multiplication in outbreak areas. The Cloncurry-Hughenden, Winton-Barcaldine, and Darling Downs outbreak areas must have been active.

The two new infestations reported in January from New South Wales are thought to have resulted from further outbreak area activity, the Culgoa-Barwon and, possibly, Bogan-Macquarie outbreak areas being involved in the north and the Bland outbreak area in the south. In these areas conditions were favourable for survival during the spring. In terms of Key's limits, most of the main area infested experienced favourable conditions in January. However, conditions were apparently sufficiently moist to cause high mortalities in some of the eastern sections. The following month (Fig. 14) the infestation persisted on the eastern side except around stations that had recorded Meyer ratios of 20.5 or more, suggesting again that the upper moisture limit at temperatures in the vicinity of 74°F. is close to 20.

February was a relatively dry month, particularly in the western parts of the area infested (Fig. 14). Swarm coherence was maintained in the south under drier conditions than in the north. In the south-western sections conditions were unfavourably dry in terms of Key's limits. Presumably the preceding rainfall had been high enough for the persistence of enough green feed to allow some swarms to maintain coherence throughout the month.

In the area between Gunnedah and Coonamble, the monthly Meyer ratios were not unfavourable for the maintenance of an infestation of the magnitude recorded. The rainfall distribution was quite favourable. Thus the failure of the outbreak there cannot be explained satisfactorily in terms of physical factors.

The local field observer reported that everywhere in his area numerous locusts were "sick" and dying, and contained "maggots." Thus it appears that parasitism caused the collapse of the outbreak in this region. It is possible that the parasite concerned was an unidentified fly (Sarcophagidae or Tachinidae) found by the author in this region during the previous season. It was the only endoparasite found in locusts in the Bogan-Macquarie and Warrumbungles outbreak areas during 1941-42, and was more numerous in the latter area. In the small samples collected there the percentage parasitism was of the order of 5-10 per cent.

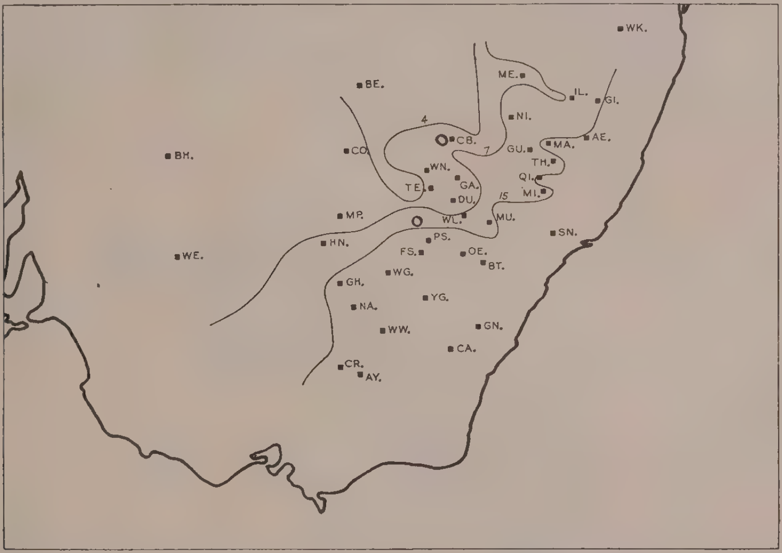

Fig. 16.—Limits of the New South Wales areas infested by swarms in September 1943, together with isopleths for Meyer ratio (symbols as before).

It may be assumed that the population density of the parasite was very low in the early summer of 1940-41 as very few locusts or other acridids were present at the time. After December 1940, one non-swarming and three swarming generations developed before the parasite became sufficiently numerous to cause a drastic reduction of locust numbers. Elsewhere, out of the radius of migration of swarms originating in the Coonabarabran P.P. District, no parasitism was reported nor was any abnormality suggesting it noted in the behaviour of locusts. Thus it may be concluded that physical factors dominated in determining the magnitude of the infestation in other parts of New South Wales. There, swarming began two generations later than in the Coonabarabran P.P. District.

As shown in Figure 15, March was a much drier month than February. The flying swarms remaining in the main area infested all disintegrated by the end of the month as a result of mortality. Except in a small area near Quirindi no hatchings were observed although numerous deposits of eggs were reported, some of which had been laid early in February. The fact that extensive hatchings of the third generation did not occur was due apparently to the dryness of the month. This fits with Key's (1942) conclusions. Moisture conditions became favourable again in April, but by this time the prevailing temperatures (55-63°F.; mean 58°F.) were too low everywhere to allow complete egg development to hatching, which did not occur until the following spring.

In terms of Key's limits, favourable conditions persisted in the Hunter River valley during March, but there also the swarms disintegrated before the end of the month, and no further hatchings were observed. The rainfall distribution for the month was examined, and it was found that approximately half the rain recorded fell at the end of the month. Thus the effective Meyer ratio for most of the month was only about half that indicated by the monthly figure, i.e. slightly over 2 and thus very close to Key's limiting value.

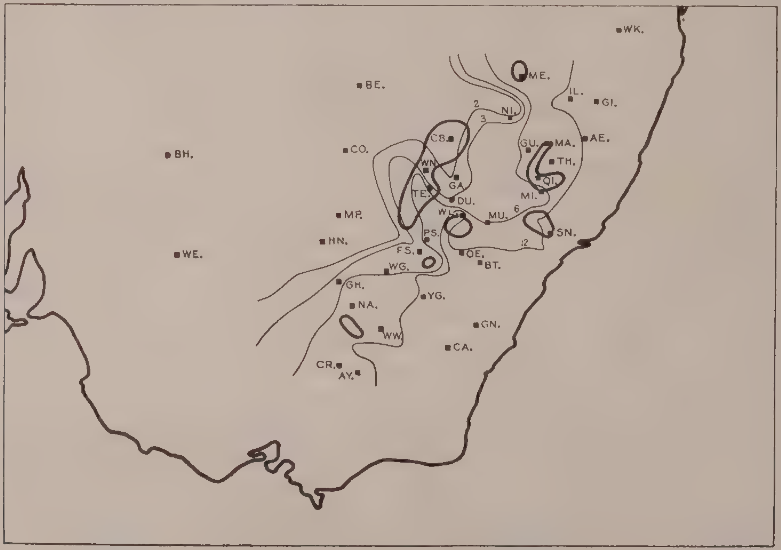

Fig. 17.—Limits of the New South Wales areas infested by swarms in October 1943, together with isopleths for Meyer ratio (symbols as before).

(*d*) *The Outbreak of* 1943-44

(i) *Description.*—A minor outbreak of *Chortoicetes* occurred during the 1943-44 locust season. As indicated in Table 5, swarms of the first generation infested a considerable area in New South Wales. The outbreak in Queensland was negligible. The first swarm hatchings in New South Wales were reported towards the end of September from west and south-west of Coonamble, and between Tullamore and Parkes (Fig. 16). Hatching continued in October and the total area infested increased greatly (Fig. 17). Swarms were reported from seven areas in New South Wales—around Moree, from Manilla to Quirindi, Hunter River valley, north of Coonamble to the vicinity of Trundle, south of Wellington, between Forbes and Canowindra, and west of Wagga Wagga.

In November (Fig. 18) flying swarms appeared south of Moree, in the Liverpool Plains area, and in the Coonabarabran, Dubbo, and Urana P.P. Districts. In the Urana area the species concerned may have been *Austroicetes cruciata* (Sauss.). Little migration was reported before the end of the month except in the Urana area. Elsewhere, with few exceptions, the adult swarms were said to be settled on the ground. Hatching continued during the month, commencing in several new areas, including the Young P.P. District, the eastern part of the Molong P.P. District, and places near Bundarra and Coolah.

TABLE 5

DETAILS OF THE 1943-44 OUTBREAK

Month	Total Number of Swarms Reported (Queensland given separately)	Total Area Infested (sq. miles) (Queensland given separately)
September	7	250
October	64 (3 Qld.)	11,750 (500 Qld.)
November	78 (? Qld.)	19,100
December	42 (4 Qld.)	3,500 (1,100 Qld.)
January	43 (5 Qld.)	3,700 (1,300 Qld.)
February	24 (1 Qld.)	2,100 (100 Qld.)
March	13	1,000
April	2	200

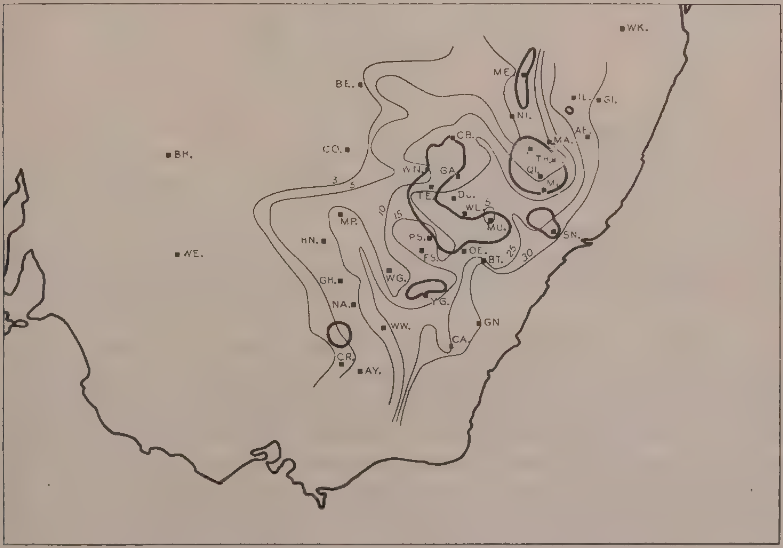

Fig. 18.—Limits of the New South Wales areas infested by swarms in November 1943, together with isopleths for Meyer ratio (symbols as before).

The outbreak continued in December (Fig. 19), but as shown in Table 5, the number of swarms reported was much lower than during the previous month. Flying and laying swarms were observed in the Hunter River valley. Egg beds and young swarm hoppers were reported from near Trangie and Narromine in the Dubbo P.P. District. These young hoppers were hatchings of the second generation. They were stated to die out rapidly because of dry conditions. Flying and settled swarms of adults were seen between Wellington and Molong. South of Mudgee flying swarms and others just moulting to the adult stage were observed. Elsewhere the outbreak had ended.

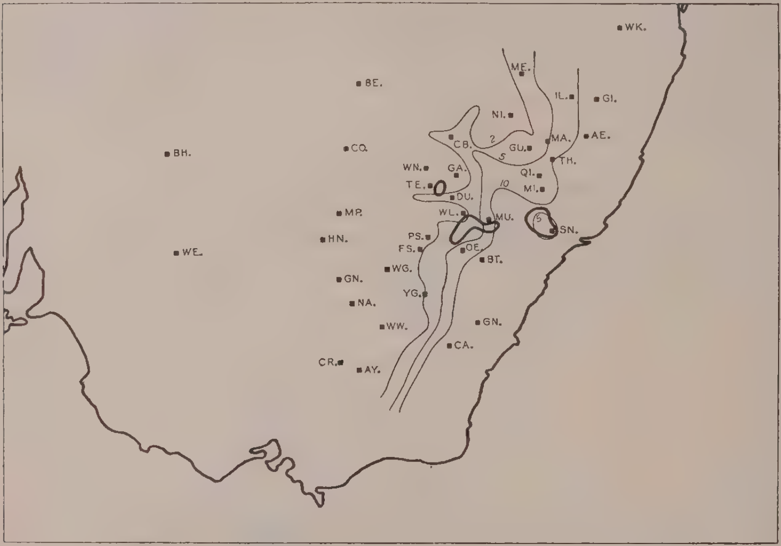

Fig. 19.—Limits of the New South Wales areas infested by swarms in December 1943, together with isopleths for Meyer ratio (symbols as before).

In January, the infestation continued in the Hunter River valley (Fig. 20). The swarms reported were either of hoppers or young fliers, indicating that the first generation had died out, and that the second had begun to hatch in December although this had not been recorded. Hatching of the second generation also began near Molong, but no swarms were produced. On January 1, young hopper swarms hatched near Trangie and Narromine but soon disintegrated. Some egg beds in this area failed to produce hoppers. Swarms just reaching the adult stage were reported east of Mudgee, but they also disappeared before the end of the month.

In February (Fig. 21) the total area infested was smaller still. Swarms of old hoppers and adults were noted in the Hunter River valley. Hopper bands were also recorded just south of Quirindi. These were of the second generation and must have hatched late in January. The following month the infestation showed a further decrease (Fig. 22). Two bands of old hoppers were reported south of Quirindi, representing survivors from the previous month. Adult swarms of the second generation persisted in the Hunter River valley and laying occurred there. Reports of adult swarms were received from Hillston and Hay, indicating the occurrence of new infestations.

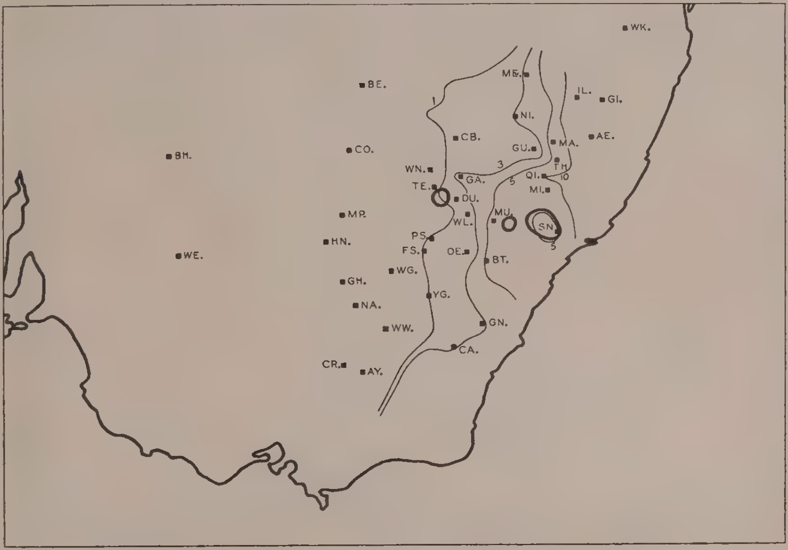

Fig. 20.—Limits of the New South Wales areas infested by swarms in January 1944, together with isopleths for Meyer ratio (symbols as before).

In April the outbreak was restricted to areas near Hillston and Hay. By the end of the month the only remaining swarms were those near Hillston, which survived into May.

(ii) *Analysis.*—The swarms that hatched during the spring of 1943-44 were only partly the progeny of swarms of the second generation of the 1942-43 season. If the area infested in February 1943 is compared with those infested subsequently in September and October 1943 (compare Figs. 14, 16, and 17), it is apparent that the hopper bands that appeared around Moree (MacIntyre-Gwydir outbreak area), west of Wagga Wagga (Riverina outbreak area), and in part of the area extending from north of Coonamble to north-west of Forbes (Bogan-Macquarie outbreak area), did not originate directly from swarms but resulted from outbreak area activity. Few swarms appeared in the area in which parasites had been numerous during the previous season, showing that the fly concerned had effectively reduced the infestation.

As shown by Figures 16 and 17, general hatching began in October, in most instances, at Meyer ratios ranging from 2 to 12, i.e. under favourable conditions in terms of Key's limits. Near Coonamble some swarms hatched at

Meyer ratios between 1 and 2, but suffered high mortalities soon after emergence, presumably because of the dry conditions. The following month (Fig. 18) swarm numbers increased, partly as a result of late hatchings and partly because some swarms missed earlier were seen for the first time.

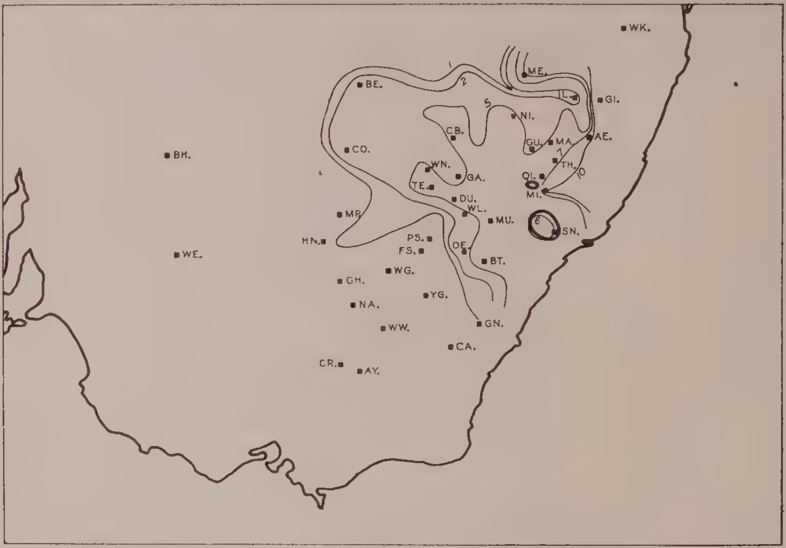

Fig. 21.—Limits of the New South Wales areas infested by swarms in February 1944, together with isopleths for Meyer ratio (symbols as before).

By early December a marked decrease had occurred in the size of the total area infested. In most places in which the infestation collapsed weather conditions were quite favourable in November. They were moist enough to ensure favourable pasture conditions into December. This was confirmed by an examination of the rainfall distribution for both months for every recording station in the region in which the swarms disintegrated. The only area in which the November moisture conditions were not much in excess of Key's lower limits was that west of Wagga Wagga. The November Meyer ratios for this area were close to those necessary for the persistence of an infestation of small, loose swarms. The few swarms in this area were the first for some time and none was stated to be either large or dense.* Their disappearance could have been caused by the prevailing moisture conditions. However, the collapse of the infestation elsewhere cannot be explained satisfactorily in terms of physical factors.

Possible other factors responsible for the decline are parasitism, predation, disease, and control campaigns. The major predators of *Chortoicetes* (birds) were not stated to be more numerous than usual or claimed to be reducing infestations. Acridid diseases appear to flourish only under very wet conditions. Very little control work was attempted because of the shortage of manpower and materials due to wartime conditions. The areas under consideration are in contact with that in which a dipterous parasite reduced an infestation effectively in 1942-43. Thus the most likely explanation of the subsequent disappearance of swarms, one locust generation later, is that the fly continued to be a major destructive factor, either as a result of spread or local multiplication. Field observations, which were very limited owing to wartime restrictions, provide no direct evidence in support of this suggestion. The fact that very few swarms were observed to migrate after reaching the flying stage suggests that they could have been heavily parasitized. The biotic factor concerned did not operate effectively in the Hunter River valley. The isolated infestation there persisted after a similar number of swarming generations.

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* It cannot be established with certainty that *Chortoicetes* was the species concerned (see last section).

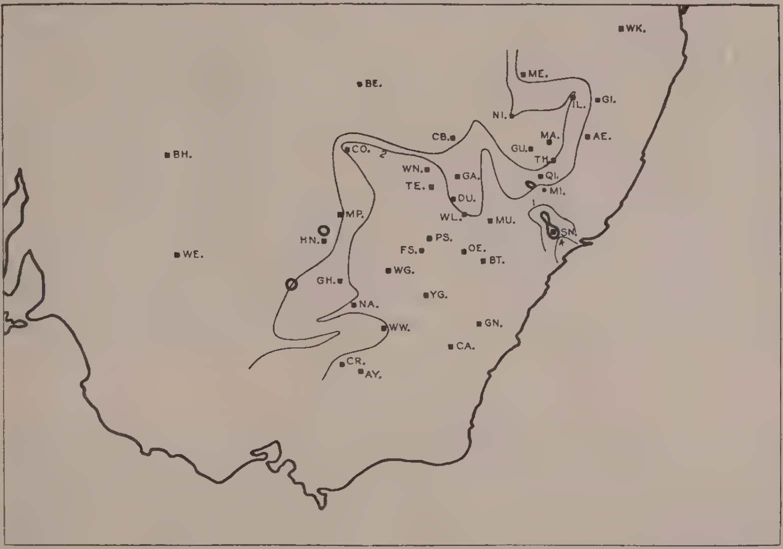

Fig. 22.—Limits of the New South Wales areas infested by swarms in March 1944, together with isopleths for Meyer ratio (symbols as before).

All the swarms present between Wellington and Mudgee died out before the end of December after a limited amount of laying. Parasites may have accelerated their end as moisture conditions were not unfavourable for the maintenance of an infestation of the magnitude indicated by the local report. The young hopper swarms recorded near Trangie died out soon after hatching, under very dry conditions.

As shown in Figure 20, apart from the Hunter River valley, the January infestation was limited to swarms near Mudgee and Narromine that disintegrated before the end of the month. Moisture conditions were favourable around Mudgee and had been so since the beginning of the season, suggesting again that parasites were playing a significant part. Around Narromine and Trangie conditions were very dry and sufficiently unfavourable to account for the high hopper mortality. Most eggs in this vicinity failed to hatch. They were laid late in November. As moisture conditions became favourable again in February (Meyer ratios 5-6) and no further hatching occurred, it may be assumed that the eggs concerned had died within 2½-3 months of laying as a result of dry conditions (see also Key 1942, 1943).

In February the infestation was limited to the Hunter River valley and a small area near Quirindi (Fig. 21), in both of which moisture conditions had been favourable throughout the season. By the end of the following month no swarms remained there, either because of the dryness of the prevailing conditions or parasitism. No further hatchings occurred before the end of the season, because conditions were first too dry and then too cold for the completion of egg development.

In March and April "light" swarms were observed in the Hillston and Hay P.P. Districts (Fig. 22). The report from Hay stated that they were settled in irrigated or "green" country. They were almost certainly of local origin as the areas concerned were far from those infested earlier in the season. The spring period in this normally arid area had been unusually wet. Localized flood rains in November doubtless aided the survival of *Chortoicetes* by providing green feed and shelter in low-lying areas during the early summer. The presence of irrigation areas may have assisted in the subsequent survival of the locusts as the later months were very dry. This is the first evidence of outbreak area country in the north-western section of the Riverina Plains. Because of the presence of favourable soil complexes in the area, Key (1945) thought it might produce swarms under exceptional moisture conditions, the normal climate being too dry.

TABLE 6

DETAILS OF THE 1944-45 OUTBREAK

Month	Total Number of Swarms Reported	Total Area Infested (sq. miles)
September	3	200 (N.S.W.)
October	14	800 (N.S.W.)
November	2	200 (N.S.W.)
December	—	—
January	—	—
February	8	1,200 (Qld.)
March	4	200 (Qld.)

(*e*) *The Outbreak of* 1944-45

(i) *Description.*—A very small outbreak of *Chortoicetes* occurred during the 1944-45 locust season in eastern Australia. Table 6 gives the monthly details of the infestation. The first swarm hatchings were observed towards the end of September in the Hunter River valley. Hatching continued during the following month, and a new area of infestation appeared between Quirindi and Gunnedah. By the beginning of November the infestation in the Hunter area had collapsed. The other area was free of swarms by the end of the month. The field observer there stated that November was very hot and dry, and that the only locusts that survived into December were those in the immediate vicinity of watercourses, creeks, and depressions, where green feed and shelter persisted longer than elsewhere. In Queensland flying swarms were recorded near Hughenden in February, and the following month a few hopper bands were reported.

(ii) *Analysis.*—The swarms which hatched in the Hunter River valley were the progeny of swarms of the 1943-44 season. Hatching began under favourable conditions in terms of Key's curve, but by the end of October high mortalities occurred and no swarms maintained coherence into the adult stage. The decline of the infestation was thought by the local observer to be due to bird predators (ibis and starlings), which were very numerous at the time. However, October was a very dry month, the Meyer ratios for both stations in the area being 0.6, a value unfavourably low for locust survival. It appears that physical factors alone could have caused the collapse of the outbreak in this area. Very dry conditions persisted until December. Numbers were reduced to such a low level that, although moisture conditions were favourable for the remainder of the season, no swarms developed.

The swarms which appeared between Gunnedah and Quirindi were probably the progeny of locusts that had been in swarms when in the hopper stage. In November 1944, when the swarms disintegrated, the Meyer ratios in the area were between 1 and 2, unfavourably low values for the persistence of swarming populations of the magnitude reported.

The available meteorological data were not adequate for an analysis of the small Queensland infestation.

IV. CONCLUSIONS

The outbreaks of *Chortoicetes* occurring during the 1940-41 and 1941-42 locust seasons were both minor in character. The first represented the end of one outbreak cycle and the second the beginning of a new one. The swarms reported during the spring of 1940-41 were the progeny of previous swarms, mainly of the second generation of the 1939-40 season. Those developing in the spring of 1941-42 resulted from the multiplication of non-swarming populations in the Bogan-Macquarie and Warrumbungles outbreak areas. These swarms appeared after one non-swarming generation, 10 months after the last record of swarms in New South Wales. In addition to these infestations in New South Wales a few swarms were reported from Queensland in 1940-41.

An extensive outbreak developed in New South Wales in 1942-43, followed by a more restricted outbreak in 1943-44, and a very limited one in 1944-45. Only very small infestations occurred in Queensland during these seasons. With the exception of the swarms that hatched in the general vicinity of the Warrumbungles outbreak area, those reported during the 1942-43 season resulted from the multiplication of non-swarming populations. Outbreak areas active in New South Wales included the Bogan-Macquarie, Warrumbungles, Hunter, Liverpool Plains, Bland, MacIntyre-Gwydir, Culgoa-Barwon, Coolah, and Inverell.

In 1943-44, the Riverina outbreak area was probably active also. The available evidence indicates the existence of additional outbreak area country in the suspected north-western section of the Riverina Plains. In Queensland, the Cloncurry-Hughenden, Winton-Barcaldine, and Darling Downs outbreak areas produced a few swarms.

In all active outbreak areas in New South Wales, except parts of the Bogan-Macquarie and Warrumbungles, three non-swarming generations occurred after the 1940-41 outbreak before swarms were produced in the spring of 1942-43. The swarms that hatched the following spring (1943-44) were partly the progeny of previous swarms and partly the result of further multiplication in outbreak areas. The few swarms observed in New South Wales during the 1944-45 season were largely the progeny of previous swarms.

Consideration of the course of these outbreaks in relation to temperature and moisture has again demonstrated the importance of these factors as determinants of the regional and seasonal occurrence of swarm populations. The curve of limiting conditions obtained by Key (1942), which defines approximately the limiting conditions of temperature and moisture at which swarms can persist, was found to be a useful guide for the interpretation of events in the present series of outbreaks. However, discrepancies occurred in a number of instances. The results of the present analysis indicate that:

(*a*) The limiting Meyer ratios for the persistence or development of a spring infestation of small, weakly gregarious swarms at temperatures between 60 and 70°F. exceed 4-5, either when the September Meyer ratio is 5 or less, or when the spring is preceded by a severe winter drought.

(*b*) The maximum Meyer ratios at which swarms can exist during the summer in northern New South Wales are in the vicinity of 20 at temperatures of 74-76°F.—a value considerably higher than that of approximately 13-14 estimated by Key.

(*c*) At the lowest temperature limit, approximately 57.5°F., swarm hatchings can occur at much lower Meyer ratios than those estimated by the other worker, e.g. 4-5 as compared with 11-12 (see also Key 1943).

Key's limiting conditions are averages derived from the various apparently limiting combinations of temperature and moisture observed by him, and in some cases are based on few data. Consequently one would expect to find discrepancies, especially in the limiting values for moisture, when using the curve to interpret particular events in the field. The present study indicates that such discrepancies could arise from a number of causes, e.g.:

(*a*) The kind of infestation concerned. The limiting moisture conditions for the persistence of dense, strongly gregarious swarms would frequently differ from those at which small, weakly gregarious swarms could survive, because the former have a greater chance of preserving coherence when the mortality rate becomes fairly high.

(*b*) The crudeness of the monthly Meyer ratio as an index of soil moisture and associated pasture conditions. The index does not take into account either the rainfall distribution of a particular month or the effect of preceding moisture conditions.

(*c*) Probable regional differences in the maximum Meyer ratios at which swarms can persist at high temperatures. It is probable that the discrepancies between the upper moisture limits recorded by Key and the present author are due to differences in the species composition etc. of the pasture vegetation in different parts of the infestation area of *Chortoicetes*.

Unlike the outbreaks of 1940-41 and 1941-42, the decline of the 1942-43 infestation in and around the Warrumbungles outbreak area cannot be explained satisfactorily in terms of physical factors, although they appeared to determine the magnitude of the outbreak elsewhere. According to the local observer in this area the swarms present were heavily parasitized by a species of fly (undetermined). It was concluded that this parasite must have been the principal destructive factor operating. It is worth noting that three swarming generations of *Chortoicetes* were completed before the parasite increased sufficiently to cause a drastic reduction of locust numbers. Similarly, during the 1943-44 season some biotic factor, possibly the same parasite, caused a great decrease in the infestation during the late spring. This collapse occurred in the third successive generation of swarms. This evidence of parasitism is of very considerable interest, and it is unfortunate that wartime restrictions limited the amount of information obtained.

V. ACKNOWLEDGMENTS

Thanks are due to Dr. K. H. L. Key, of C.S.I.R.O., for many useful discussions concerning locust outbreaks, and to those officers of State Agricultural Departments who kept the Locust Information Services going during the war. Mrs. Betty Rankin re-drew my maps for publication.

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OBSERVATIONS ON THE BIOLOGY OF *LYCTUS BRUNNEUS* (STEPH.)

By F. J. Gay*

[*Manuscript received February* 14, 1952]

Summary

An account is given of certain aspects of the biology of *Lyctus brunneus* (Steph.).

Female beetles are able to oviposit within 24 hr. after emerging from infested timber and deposit an average of more than 70 eggs per female over a period of 1-2 weeks. Eggs are deposited at depths of 1.0-6.5 mm. in the wood vessels, preferentially from a transverse surface, but also through radial and tangential faces.

The incubation period of the eggs ranges from about 1 week at 26°C. to 3 weeks at 15°C. The egg-adult developmental period ranges from 4 months at 26°C. to 16 months or more at 15°C. Under optimal conditions of temperature, relative humidity (and hence wood moisture content), and nutrition, the life cycle may be as short as 2 months.

The sex ratio of *L. brunneus* is 1 : 1 and the adult beetles live from 2½ to 7 weeks, depending upon the temperature, females being somewhat longer-lived than males.

The larvae of *L. brunneus* are somewhat more resistant to heat treatment than are the eggs, but one ½-hr. exposure to 50°C. is completely lethal to both stages.

I. INTRODUCTION

The tremendous demand in Australia for timber for general constructional work, furniture, joinery, etc. has resulted in the increasing use of a number of timbers that formerly were either milled in only small quantities or were used solely as case timbers. These timbers, most of which are rain-forest species, frequently possess a wide sapwood containing quantities of starch, and are therefore readily susceptible to the attack of *Lyctus* beetles.

The growing seriousness of the *Lyctus* problem has been responsible for the formulation of a cooperative research programme between the Divisions of Forest Products and Entomology, C.S.I.R.O., the Division of Wood Technology of the New South Wales Forestry Commission, and the Forest Products Research Branch of the Queensland Forest Service. The observations recorded in this paper represent a contribution by the Division of Entomology to this cooperative research scheme.

In Australia the principal species of *Lyctus* responsible for damage to the sapwood of hardwoods is the introduced cosmopolitan *L. brunneus* (Steph.). Although some detailed studies of the biology of this species have been carried out overseas, notably by Parkin (1934), no similar work has been done in Aus-

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tralia. The following investigations were made in order to remedy this lack and to supply additional data on particular points of the insect's biology that might have a bearing on its control.

II. OVIPOSITION

The pre-oviposition period appears to be relatively short and only to occupy the few days the adult beetle spends within the pupal cell whilst its cuticle is hardening and darkening. Newly emerged beetles, that is individuals that have made their way out of the timber in which they have developed, are able to mate and lay fertile eggs within 24 hr. of emergence.

The eggs are deposited within the vessels of the wood, generally two or three eggs being placed one behind the other in the lumen of the vessel. The depths at which the eggs are laid are surprising when considered in relation to the size of the insect and have an important bearing on the desirable depth of penetration of preservative treatments.

The depth of oviposition in seven species of timber was determined by exposing ½-in. cubes of each timber to 10 male and 10 female *L. brunneus* for periods of 3 or 4 days and subsequently sectioning these blocks under the microscope and measuring the depths at which eggs occurred. The measurements were made from the mid point of the egg (which is about 1 mm. long) and are given to the nearest 0.25 mm. Tangential and radial faces of the blocks were masked in order to restrict oviposition to the transverse surfaces of the blocks. The results of this series of tests are summarized in Table 1. It will be seen from this table that in all seven timbers some eggs are laid at depths in excess of 5 mm. One anomalous record was the occurrence in *Eucalyptus obliqua* of an egg at a depth of 7.75 mm. from the surface. This egg, however, was loose in the lumen of the vessel and had apparently slipped down and become lodged at this point. Such an occurrence is unusual and was only observed once in measuring almost 500 eggs.

TABLE 1

DEPTH OF OVIPOSITION BY *L. BRUNNEUS* IN VARIOUS TIMBERS

Timber	No. of Eggs Measured	Depth of Oviposition Range (mm.)	 75 per cent. Zone* (mm.)
Schizomeria ovata	60	1.75-5.5	2.25-4.50
Eucalyptus obliqua	52	2.00-5.25	3.00-5.00
Eucalyptus maculata	80	1.00-6.50	2.00-5.00
Alstonia scholaris	103	2.00-5.75	3.00-5.50
Sterculia acerifolia	70	1.25-5.50	2.00-5.00
Sloanea woollsii	60	1.00-5.50	2.00-4.50
Tarrietia argyrodendron	60	1.75-5.25	2.75-4.50

* Range over which 75 per cent. or more of the eggs occurred.

Because of the habit of ovipositing in the vessels it was thought that exposed transverse surfaces of timber would be favoured by egg-laying females. This point was checked by exposing ½-in. cubes of three species of timber to groups of five male and five female *L. brunneus* for 24 hr. at 26°C. These blocks were sectioned after a lapse of 3 weeks and counts made of the numbers of young larvae present. Although this method does not allow for any egg mortality it is considered adequate for this investigation. Six cubes of each timber species were used, two with only the transverse faces exposed, two with the radial faces only, and two with the tangential faces only. The results are given in Table 2.

TABLE 2

EFFECT OF WOOD SURFACE ON OVIPOSITION OF *L. BRUNNEUS*

Timber	Larvae Present in Blocks with					
	Exposed Transverse Faces		Exposed Radial Faces		Exposed Tangential Faces	
	A	*B*	*A*	*B*	*A*	*B*
Schizomeria ovata	62	—	51	35	31	30
Sterculia acerifolia	62	62	19	0	0	13
Alstonia scholaris	65	77	53	22	61	46

It will be seen that, in each of the three timber species, oviposition can occur on any of the three possible exposed faces. Oviposition is heaviest on the transverse face, but, nevertheless, appreciable egg laying is possible on both radial and tangential faces. Such oviposition may take place in the ends of vessels exposed owing to obliqueness of the grain, but eggs are also laid in the lumen of vessels exposed by the mandibular action of the adult beetles. These "tasting marks," which have been referred to by Parkin (1936), appear to have a dual function for, in addition to enabling the female beetle to select suitable starch-containing wood for oviposition, they expose the ends of vessels in which eggs can be laid. Although Parkin tends to discount the possibility of oviposition occurring in this way, newly hatched larvae were repeatedly found in close proximity to such marks, indicating that eggs had been laid at these sites.

III. NUMBER OF EGGS

The number of eggs laid by a female of *L. brunneus* is generally stated to be fairly low and Parkin (1934) quotes figures of an average of 17.4 eggs for 12 females in one test and 21.2 eggs for 18 females in another test. These averages are surprisingly low and well below the potential per female based on ovarian counts; Parkin's figures for the latter are 56-84 eggs per female, with an average of 70. The discrepancy may be due to the fact that his figures for the number of eggs laid by a female were obtained by counting the exit holes in pieces of oak sapwood on which the females had been allowed to oviposit. This method does not take into account egg, larval, or pupal mortality and may underestimate the actual oviposition quite considerably.

This question of the number of eggs per female has been re-examined using a method that not only eliminated errors due to larval and pupal mortality but enabled the pattern and duration of oviposition to be observed.

Newly emerged virgin females were isolated in containers with a single male and supplied with a fresh ½-in. cube of susceptible sapwood every 24 hr. The pairs of beetles were maintained at 26°C. and 75 per cent. relative humidity and the blocks, after removal, incubated under these conditions for 1 month before being sectioned and examined for larvae.

The complete oviposition histories of 25 females were obtained and the following are the principal points recorded. The total oviposition ranged from 0 to 221 eggs, the individual totals being 0, 1, 1, 26, 32, 32, 35, 42, 49, 50, 52, 53, 70, 72, 82, 90, 92, 98, 102, 109, 111, 120, 155, 205, and 221. This gives an average of 76 eggs per female, which is considerably greater than either of the figures quoted by Parkin, and much closer to the 70 per female based on ovarian counts. The maximum period over which egg laying extended was 22 days, but in most instances it lasted only 1-2 weeks with the majority of the eggs being laid within the first 7-8 days of the female's life. Most of the females lived for several days after oviposition had ceased, and subsequent dissection showed that 40 per cent. of these females still had unlaid eggs present in the egg calyces. The number of such unlaid eggs ranged from 4 to 25.

All females that laid eggs began ovipositing within the first 24 hr. after emergence and in a majority of instances the highest single daily egg deposition occurred in this first 24-hr. period. The greatest number of eggs deposited by one female in a day was 37.

Dissection of newly emerged females showed from 20-80 eggs present in the calyces (the average for 14 females was 48 eggs). These evidently are the eggs that are laid during the first few days of the oviposition period, after which the primordia visible in the ovarioles develop into additional eggs. The relationship between potential and actual eggs laid, on the basis of the above figures, shows none of the anomalies evident in Parkin's data and it is clear that his method for determining actual progeny was inadequate.

IV. Length of Developmental Period

The incubation period of the eggs was 6-7 days at 26°C., 12-13 days at 20°C., and 19-20 days at 15°C. In the same way, the length of the developmental period from egg to adult is influenced by the temperature and to a somewhat lesser extent by the relative humidity. The amount of this variation may be gauged from Table 3, which presents in summary the results of a number of tests in which *L. brunneus* was reared at various combinations of temperature and relative humidity (and hence, wood moisture content). For the purposes of these observations, 1¼ by 1 by ½ in. blocks of *Alstonia scholaris* sapwood, with a high starch content, were conditioned at the appropriate temperature and relative humidity for 2 weeks. All blocks were then exposed to five pairs of *L. brunneus* for 24 hr. at 26°C. and 75 per cent. relative humidity in order to ensure as uniform oviposition as possible. The beetles were removed and the blocks incubated to complete emergence, under the same conditions of temperature and relative humidity as during the pre-oviposition conditioning.

It will be seen from Table 3 that development is very slow at 15°C., requiring a minimum of about 16 months for the completion of the egg-adult stage. An increase in temperature of 5°C. to 20°C. reduces this period to 5-6 months, whilst a further increase of 6°C. to 26°C. reduces the time to approximately 4 months. This appears to be close to the optimum temperature for this species, a suggestion supported by the fact that at each relative humidity level many more beetles emerged at 26°C. than at the other temperatures studied. At 30°C. very few insects were able to complete their development and those that did so took about 6 months. It is interesting to note that at this temperature the eggs hatched and the larvae developed quite successfully, pupation appeared to take place quite normally, but heavy mortality occurred in the pupal state and relatively few adults emerged from the pupae.

TABLE 3

AVERAGE LENGTH OF EGG-ADULT DEVELOPMENTAL PERIOD (DAYS) OF *L. BRUNNEUS* AT VARIOUS COMBINATIONS OF TEMPERATURE AND RELATIVE HUMIDITY

Relative Humidity	15°C.	20°C.	26°C.	30°C.
20%	No development after 19 months	No development	194.6 (28 ♂ ♂) 190.2 (19 ♀ ♀) 192.8 (both sexes)	—
40%	485.2 (12 ♂ ♂) 535.7 (9 ♀ ♀) 506.9 (both sexes)	150.4 (42 ♂ ♂) 150.3 (31 ♀ ♀) 150.4 (both sexes)	127.8 (76 ♂ ♂) 121.3 (75 ♀ ♀) 124. 6 (both sexes)	No development
60%	529.3 (13 ♂ ♂) 517.3 (14 ♀ ♀) 523.1 (both sexes)	157.8 (46 ♂ ♂) 157.4 (49 ♀ ♀) 157.6 (both sexes)	118.6 (76 ♂ ♂) 116.8 (67 ♀ ♀) 117.7 (both sexes)	—
65%	483.2 (20 ♂ ♂) 471.4 (29 ♀ ♀) 476.2 (both sexes)	—	—	177.4 (7 ♂ ♂) 188.6 (3 ♀ ♀) 180.8 (both sexes)
80%	466.7 (9 ♂ ♂) 497.8 (9 ♀ ♀) 482.3 (both sexes)	176.8 (41 ♂ ♂) 178.0 (44 ♀ ♀) 177.4 (both sexes)	115.3 (70 ♂ ♂) 112.2 (73 ♀ ♀) 113.7 (both sexes)	—
100%	No emergence after 20 months; living larvae present	—	No development; heavy mould growth	No development

Extremely low and high humidities are deleterious, the former probably because of desiccation effects and the latter because of fungal activity. Over the range 40-80 per cent. relative humidity, however, development was possible without any definite correlation with the length of the developmental period being evident.

It is clear from the above figures that the length of the developmental period is generally considerably over-estimated in literature. The most frequently quoted period is 1 year from egg to adult, whereas under favourable conditions it may be only 4 months. However, if conditions are optimal rather than favourable the minimum developmental period may be reduced to as little as 2 months. This speeding up in development appears to depend on nutritional rather than physical factors as is indicated by the following data obtained from rearing laboratory cultures of *L. brunneus* over a period of more than 3 years. These cultures are maintained at 26°C. and 75 per cent. relative humidity and the timbers used as food material are *Schizomeria ovata, Alstonia scholaris,* and *Sterculia acerifolia,* all of which are highly susceptible species normally containing abundant starch in the sapwood. The time from the first oviposition to the emergence of the first progeny (i.e. the minimum developmental period) varied quite significantly, however, despite the fact that all factors, other than the timbers themselves, were kept constant. The range for 111 blocks of *Schizomeria ovata* was 88-234 days for the minimum developmental period with an average of 146 days. *Alstonia scholaris* (120 blocks) had a range of 70-120 days with an average of 92 days, and 127 blocks of *Sterculia acerifolia* had a range of 63-114 days with an average of 75.5 days. These differences in the minimum developmental period are most probably due to variations in the quantity and availability of starch (although this was not apparent from visual grading after staining with iodine) or of some other essential food material.

V. SEX RATIO

The sex ratio of *L. brunneus,* as determined from almost 45,000 beetles reared during the past 3 years, is practically 1 : 1, the actual numbers being 22,587 females to 22,021 males.

VI. LENGTH OF ADULT LIFE

The length of life of the adult beetles varies considerably and is determined to a marked degree by the temperature. A series of tests on adult longevity at 15°, 26°, and 30°C. is summarized in Table 4.

It will be seen from this table that some adults die soon after emergence, but that adult life may last up to 12 weeks. Then length of life is reduced as the average temperature rises and, at all temperatures studied, female beetles live somewhat longer than males. The above figures agree quite well with those quoted by Parkin (1934).

VII. TEMPERATURE TOLERANCE OF EGGS AND YOUNG LARVAE

This investigation was made in order to obtain more precise information on the temperatures and exposures necessary to ensure an effective kill by means of heat sterilization (kiln treatment).

The technique used for determining the thermal death point of the eggs was as follows. Small blocks of *Alstonia scholaris* sapwood, each 1 by ½ by ¼ in. were exposed to five pairs of *L. brunneus* beetles for 24 hr. The beetles were then removed, the blocks divided into halves, one of which was incubated at

26°C. without further treatment, whilst the other half was transferred to a constant-temperature container submerged in a water-bath. After the appropriate exposure period the half blocks were removed from the water-bath and incubated at 26°C. Both heat-treated and untreated blocks were sectioned after 3 weeks and examined for the presence of living larvae.

In carrying out the tests on the larvae, the small blocks were incubated at 26°C. for 3 weeks before being halved. One half of each block was incubated for a further 4 days and then examined for living larvae, whilst the remaining half was heat treated, then examined for the presence of living larvae after a lapse of 2 days.

TABLE 4

LONGEVITY OF ADULT *L. BRUNNEUS* AT VARIOUS TEMPERATURES

Twenty-five individuals of each sex were observed in each test

	Males		Females	
Temperature and Relative Humidity	Range (days)	Mean (days)	Range (days)	Mean (days)
15°C., 60%	3-58	35.7	20-84	49.1
26°C., 75%	6-33	20.2	13-34	22.4
30°C., 60%	1-27	16.8	12-26	19.8

The presence of living larvae in a half block that had not been subjected to heat treatment was regarded as evidence that the corresponding heat-treated half had contained living eggs or larvae before treatment. All blocks used in these tests fulfilled this requirement.

It should be pointed out that in these tests no attempt was made to control the relative humidity. However, the initial moisture content of the test blocks was approximately 12 per cent. and, since this moisture content represents the equilibrium condition for *A. scholaris* exposed to a relative humidity of 50-60 per cent. (depending on the temperature), the relative humidity within the sealed container cannot have exceeded this figure.

Duplicate tests of both eggs and larval blocks were made for each exposure at the various temperature levels and the results of the two groups of tests are summarized in Table 5.

The main points are clear, firstly the time of exposure necessary to give a complete kill of eggs and young larvae decreased with increasing temperature until at 50°C. a complete kill of both stages was obtained with only one ½-hr. exposure; and secondly, the larvae were somewhat more resistant to heat treatment than the eggs.

On general grounds one would expect that with larger samples for each trial there would be a tendency for a general shift towards longer periods of exposure at a constant temperature or to higher temperatures at a constant exposure to give 100 per cent. kill. It was not feasible to make an exact count of the number of eggs or larvae present but, as about 100 individual eggs or larvae were exposed to risk in each treatment, it seems unlikely that the limits, as given by this series of trials, could be materially altered by increasing the sample size.

TABLE 5

RESULTS OF TESTS OF THE TEMPERATURE TOLERANCE OF EGGS AND LARVAE OF *L. BRUNNEUS*

L = some eggs or larvae alive
D = all eggs or larvae dead

Exposure	37.5°C.		40.0°C.		42.5°C.		45.0°C.		47.5°C.		50.0°C.	
(hr.)	A	B	A	B	A	B	A	B	A	B	A	B
0.5									D	D	D	D
1	L	L	L	L	L	L	L	L	D	D	D	D
1.5											D	D
2	L	L	L	L	L	L	L	L	D	D	D	D
3									D	D	D	D
4	L	L	L	L	L	L	D	D	D	D		
6							D	D				
8	L	L	L	L	D	D	D	D				
24	L	L	L	D	D	D						
0.5									L	L	D	D
1	L	L	L	L	L	L	L	L	D	D	D	D
1.5											D	D
2	L	L	L	L	L	L	L	L	D	D	D	D
3									D	D	D	D
4	L	L	L	L	L	L	D	D	D	D		
6							D	D				
8	L	L	L	L	L	L	D	D				
24	L	L	L	L	D	D						

VIII. DISCUSSION

The present investigations serve to emphasize the fact that the reproductive potential of *L. brunneus* is much higher than is generally supposed. Not only are the females able to lay more eggs than previous records indicate, but the length of the developmental period, under favourable conditions, may be less than one-quarter of that given in most publications. These findings are significant in relation to the occurrence of *L. brunneus* in the more northern parts of Australia and indicate that in north Queensland, for example, the economic importance of this insect may very well be greater than originally expected.

Mention has already been made of the significance of the depth of oviposition in relation to the penetration of preservative treatments. It is clear from the foregoing account that any treatment that does not penetrate at least ¼ in. cannot be expected to make the timber completely immune to attack. This fact has been recognized already by some workers and in a recent publication by Tooke (1949), in discussing pre-treatment with pentachlorphenol solutions to prevent *Lyctus* attack, he states, "These requirements should be strictly adhered to if the desired results are to be obtained . . . a minimum sapwood penetration of 1/3 in." He also specifies this depth of penetration as that necessary for satisfactory results with copper naphthenate.

IX. ACKNOWLEDGMENT

My thanks are due to Miss B. J. Gemmell for technical assistance throughout the course of these observations.

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THE AUSTRALIAN SPECIES OF *APONOMMA* AND *AMBLYOMMA* (IXODOIDEA)

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Summary

A study has been made of the Australian species of *Aponomma* and *Amblyomma* (Ixodoidea).

Nine species of *Aponomma* were determined, namely *A. trachysauri, A. hydrosauri, A. auruginans, A. decorosum, A. simplex, A. trimaculatum, A. tachyglossi, A. tropicum,* and *A. pulchrum,* the last three species being new. Two previously described species, namely *A. quadratum* and *A. ecinctum,* were not recognized among the material available for study. A detailed description is given of each species together with essential figures. Keys to the males, females, and nymphs are included.

Twelve species of *Amblyomma* were seen. Species previously described included *A. moreliae, A. limbatum, A. albolimbatum, A. triguttatum, A. australiense,* and *A. papuana. A. postoculatum* and *A. helvolum* were not recognized among the material available for study. *A. papuana* is recorded from Australia for the first time. Four new species, namely *A. sternae, A. echidnae, A. macropi,* and *A. moyi,* are described. Keys to the males and females are given.

INTRODUCTION

The 40 species of ticks which have been reported from Australia are included in the following genera: *Argas* (3), *Ornithodoros* (2), *Ixodes* (11), *Haemaphysalis* (5), *Rhipicephalus* (1), *Boophilus* (1), *Indocentor* (1), *Hyalomma* (1), *Aponomma* (8), and *Amblyomma* (7), the number of species in each genus being shown in parenthesis.

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Indocentor atrosignatus (Neumann 1906), from an unknown host, was doubtfully recorded as Australian. There has been no confirmation of its occurrence in Australia but Taylor (1946) has recorded it from the wild pig in Dutch New Guinea.

Cleland (1910) reported *Hyalomma aegyptium* (Linn. 1758) from the camel, horse, and ox in Western Australia. The collection of the Animal Health Station, Yeerongpilly, Queensland, includes three tubes of material each comprising a single female labelled as *H. aegyptium* and taken from the horse, ox, and sheep respectively in unknown localities between 1902 and 1912. Taylor (1911) recorded this tick from the dog at Townsville, Queensland, but some of the material identified by Taylor as *H. aegyptium* is actually *Rhipicephalus sanguineus* (Latreille 1804). The same author (1946) reported *H. aegyptium* from the ox, horse, wild pig, sheep, dog, cat, and man in New South Wales, but this record also seems erroneous and originated from a misinterpretation of Fielding's (1926) discussion on this species, in which he dealt with its distribution and hosts in Africa, Asia, and Europe. A species of *Hyalomma* may still be present in Australia, but, if so, it has not been found in eastern Australia.

The two species of *Ornithodoros*, namely *O. gurneyi* Warburton 1926 and *O. talage* (Guerin-Meneville 1849), can be readily determined from the available descriptions. Little difficulty is also experienced in identifying the common cattle tick, *Boophilus microplus* (Canes. 1887), and the widespread dog tick, *R. sanguineus* (Latreille 1804).

The species of *Argas, Ixodes,* and *Haemaphysalis* have been defined in a series of monographs by Nuttall *et al.* (1908) and Nuttall and Warburton (1911, 1915); the keys and descriptions given by these authors are adequate for identifications. The species of *Amblyomma* were revised by Robinson (1926) but, because of the variations that occur in some species, identifications via Robinson's keys and descriptions are unsatisfactory.

No serious attempt has been made to study the taxonomy of the species of *Aponomma* since Neumann's (1899) revision. Rainbow (1906), Ferguson (1925), and Fielding (1926) included this genus in their studies of Australian ticks, but these papers were compiled mainly from the literature and not from personal examination of material.

The Australian species of *Amblyomma* and *Aponomma* occur usually on native fauna. Specimens are occasionally taken from domestic animals, however, and the difficulty experienced in determining these prompted the writer to carry out this revision.

Detailed descriptions of all the species of *Aponomma* have been attempted. Where a species of *Amblyomma* has been described by Robinson (1926), the writer has been content to record any variations from Robinson's descriptions that were encountered. New species have been described in detail.

The material on which this revision is based came from the collections of the Entomological Department of the University, the Animal Health Station, Yeerongpilly, Department of Agriculture and Stock, and the Queensland Museum, Queensland; of the Department of Agriculture, The Australian Museum, the School of Public Health and Tropical Medicine, University of

Sydney, New South Wales; of the National Museum, Melbourne; of the South Australian and Tasmanian Museums; and of the Department of Agriculture, Western Australia.

The terms for the various morphological structures used in the descriptions given in this paper are those set down by Nuttall and Warburton (1911) and Robinson (1926). Body length measurements are from the tips of the scapulae to the posterior margin of the body. Body width is the maximum width. Scutal dimensions include the length from the tips of the scapulae to the posterior angle and the width between the lateral angles.

Genus *APONOMMA* Neumann

1899 *Aponomma* Neumann, p. 180.

The genus *Aponomma* possesses the following characters: body, particularly in the male, frequently subcircular; scutum frequently ornate or with different shades of brown; eyes absent; capitulum long; spiracular plates subtriangular with rounded angles or comma-shaped; festoons present; anal groove encircling the anus behind; tarsi frequently humped; male without adanal plates, but small ventral plaques may be present close to festoons.

Neumann (1899) recorded the following species of *Aponomma* from Australia: *A. hydrosauri* (Denny 1843), *A. trachysauri* (Lucas 1861), *A. decorosum* (Koch 1867), *A. trimaculatum* (Lucas 1878), and *A. concolor* Neumann 1899. *A. ecinctum* Neumann 1901 was added later, and in 1905 Neumann decided that *A. hydrosauri* and *A. concolor* were synonymic. Cooper and Robinson (1908) described *A. simplex* and *A. quadratum*, and *A. auruginans* was added by Schultz (1936).

Nine species have been recognized in the present study, namely *A. trachysauri, A. hydrosauri, A. auruginans, A. decorosum, A. simplex, A. trimaculatum, A. pulchrum, A. tachyglossi*, and *A. tropicum*, the last three species being new. *A. ecinctum* and *A. quadratum* were not recognized in the collections examined.

These species occur normally on various species of Reptilia, on the spiny ant-eater, and on the wombat. Four species, *A. trimaculatum, A. simplex, A. hydrosauri*, and *A. tachyglossi*, have each been collected on a single occasion from the larger domestic animals; otherwise this genus has no economic importance in Australia.

These nine species fall into three well-defined groups. The first group includes *A. trachysauri, A. hydrosauri, A. tachyglossi, A. auruginans*, and *A. tropicum*, all of which are inornate and possess 2 short but strong spurs on each of the first pair of coxae and, usually in the females, an indentation of the scutal margin immediately below the lateral angle. Where the males are known, e.g. *A. trachysauri, A. hydrosauri*, and *A. auruginans*, a marginal groove is present, although somewhat ill defined in *A. auruginans*. The second group consists of *A. simplex, A. trimaculatum*, and *A. pulchrum*, both sexes of which are ornate and have only 1 spur on coxa I. There is no marginal groove in the male, nor any indentation of the postero-lateral margin of the scutum in the female. *A. decorosum* is the sole representative of the third group and in this species the scutal ornamentation is whitish, contrasting with a rich reddish brown and without any metallic sheen; coxa I has 2 spurs and the male has a well-marked, but incomplete, marginal groove.

KEY TO AUSTRALIAN SPECIES OF THE GENUS APONOMMA

*Males**

1. Marginal groove well developed, but not necessarily complete 2
   Marginal groove ill defined or absent 4

2 (1). Hypostome dentition 4/4; 5 ventral plaques present .... *A. trachysauri*
   Hypostome dentition 3/3; no ventral plaques present 3

3 (2). Scutum brownish, inornate; marginal groove complete .... *A. hydrosauri*
   Scutum deep reddish brown with extensive whitish markings; marginal groove not complete .... *A. decorosum*

4 (1). Nine shallow, symmetrically arranged depressions on posterior half of scutum .... *A. quadratum*
   No such depressions 5

5 (4). Hypostome dentition 4/4 6
   Hypostome dentition less than 4/4 8

6 (5). Inornate species .... *A. ecinctum*
   Ornate species 7

7 (6). Body never less than 2.0 mm. long .... *A. simplex*
   Body less than 2.0 mm. long .... *A. trimaculatum*

8 (5). Ornate; hypostome dentition 3/3 .... *A. pulchrum*
   Inornate; hypostome dentition 2/2 .... *A. auruginans*

Females†

1. Hypostome dentition 4/4 2
   Hypostome dentition less than 4/4 6

2 (1). Scutum with 3 metallic greenish markings 3
   Scutum without such markings 4

3 (2). Scutum conspicuously broader than long .... *A. simplex*
   Scutum about as long as broad .... *A. trimaculatum*

4 (2). Coxa I with 1 spur .... *A ecinctum*
   Coxa I with 2 spurs 5

5 (4). Porose areas subtriangular .... *A. tachyglossi*
   Porose areas subcircular .... *A. trachysauri*

6 (1). Hypostome dentition 2/2 .... *A. auruginans*
   Hypostome dentition 3/3 7

7 (6). An ornate species, with 3 metallic greenish markings .... *A. pulchrum*
   No such markings 8

8 (7). Scutum dark reddish brown, the area between the cervical grooves white .... *A. decorosum*
   Scutum brownish without such a whitish area 9

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* The males of *A. tachyglossi* and *A. tropicum* are unknown.

† The female of *A. quadratum* is unknown.

9 (8). Scutum at least 1.7 mm. long ....*A. hydrosauri*
Scutum at most 1.6 mm. long ....*A. tropicum*

Nymphs[*]

1. Hypostome dentition 3/3 2
Hypostome dentition 2/2 4

2 (1). Postero-lateral margin of scutum with a conspicuous indentation below
the lateral angle ....*A. trachysauri*
Postero-lateral margin of scutum without such indentation.. 3

3 (2). Postero-lateral margins of scutum straight or slightly concave..........*A. simplex*
Postero-lateral margins of scutum slightly convex................*A. trimaculatum*

4 (1). Scutum almost as long as wide.. ....*A. auruginans*
Scutum much wider than long......................... 5

5 (4). Cervical grooves continued by deep, strongly divergent depressions,
which reach the scutal margin............................*A. hydrosauri*
Cervical grooves continued by slightly divergent depressions, which
become shallow and do not reach the scutal margin............*A. decorosum*

Description of Species

APONOMMA TRACHYSAURI (Lucas)

Plate 1, Figs. 2, 3; Fig. 1*a-j*

1861 *Ixodes trachysauri* Lucas, p. 125.
1899 *Aponomma trachysauri* (Lucas), Neumann, p. 191, figs. 43-45.
1913 *Aponomma trachysauri* (Lucas), Patton and Cragg, p. 623.
1925 *Aponomma trachysauri* (Lucas), Ferguson, p. 34.
1926 *Aponomma trachysauri* (Lucas), Fielding, p. 88, fig. 34.
1932 *Aponomma trachysauri* (Lucas), Johnston, p. 62.
1938 *Aponomma hydrosauri* (Denny), Tubb, p. 346, fig. 1.

Larva

Diagnosis

Scutum 0.37 by 0.5 mm., broader than long; cervical grooves continuing into conspicuous depressions; hypostome dentition 2/2; coxa I with 2, short, subequal spurs, coxae II-IV each with a single spur.

Description

Body.—Pale, circular to broadly oval, 1.41-2.17 by 1.15-1.7 mm.

Scutum.—Size 0.37 by 0.5 mm., broader than long and broadest medianly, the posterior angle very broad and rounded, the postero-lateral margins concave; numerous closely set, fine, shallow pits, more uneven laterally to give a finely rugose appearance, a few larger, widely scattered punctations; cervical grooves continuing into conspicuous depressions, divergent and shallowing posteriorly to reach the postero-lateral margins.

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[*] The nymphs of *A. tachyglossi*, *A. tropicum*, and *A. pulchrum* are unknown.

Capitulum.—Length 0.21-0.25 mm.; basis 0.20 mm. wide, almost triangular in shape; palpi 0.20 mm. long, article 2 about twice the length of article 3 (0.075 mm. long); hypostome dentition 2/2 of 5 or 6 strong teeth in each file.

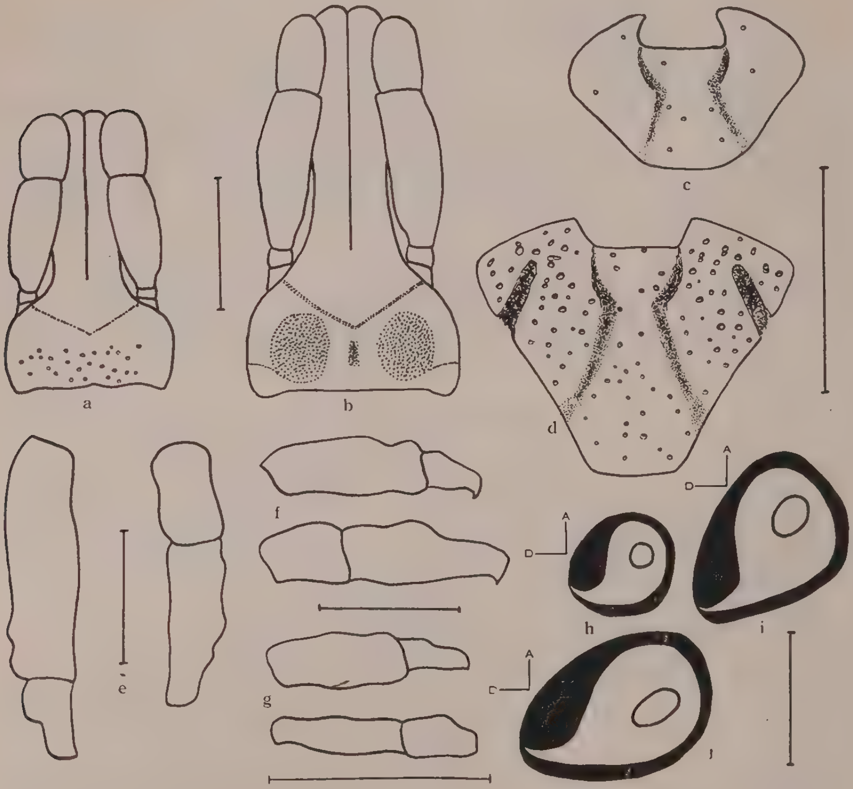

Fig. 1.—*Aponomma trachysauri*. *a*, Capitulum of male (dorsal view); *b*, capitulum of female (dorsal view); *c*, scutum of larva; *d*, scutum of nymph; *e*, tarsi I and IV of female; *f*, tarsi I and IV of male; *g*, tarsi I and IV of nymph; *h*, spiracular plate of nymph; *i*, spiracular plate of female; *j*, spiracular plate of male. The straight lines each represent 0.5 mm.

Legs.—Coxal spurs small, but similar to those of the male; tarsi without humps or spurs.

Nymph

Diagnosis

Scutum 0.68-0.8 by 1.0-1.2 mm., much broader than long, a conspicuous indentation on its margin below the eye; hypostome dentition 3/3; coxal spurs as in larva; tarsus I with a small, subterminal hump, tarsi II-IV without any hump; no tarsal spurs.

Description

Body.—Pale, with very short, scattered, pale hairs; subcircular, 1.7-4.6 by 1.9-4.3 mm.

Scutum.—Size 0.67-0.8 by 1.0-1.2 mm., broader than long and broadest in its anterior third; brown, the median region paler; posterior angle relatively narrow, postero-lateral margins sinuous; punctations in median field small and scattered, a little more numerous in posterior field, which is sometimes a little rugose, lateral fields rugose with irregular punctations and with a long, conspicuous indentation of the scutal margin just below the lateral angle; cervical grooves comma-shaped and convergent, continued posteriorly to the scutal margin by divergent and, usually, well-marked depressions.

Capitulum.—Length 0.5-0.6 mm.; basis 0.37-0.4 mm. wide; palpi 0.37-0.4 mm. long; hypostome dentition 3/3 of 5-7 teeth, the inner file with small, delicate teeth.

Spiracular plate.—Shape as in Figure 1*h*; 0.25-0.3 by 0.20-0.25 mm.

Legs.—Coxal spurs as in male, but much smaller; tarsus I 0.45 mm. long, with small, subterminal hump; other tarsi 0.3-0.4 mm. (tarsus IV) long without any obvious humps, no spurs.

Male

Diagnosis

A rather large tick; subcircular; scutum inornate, markedly rugose; marginal groove deep and complete; 5 small, ventral plaques; basis capituli with shallow, rounded cornua; hypostome dentition 4/4; coxa I with 2 short, subequal spurs, coxae II-IV each with one spur; tarsi humped and with terminal spurs.

Description

Body.—Size 3.16-4.0 by 3.16-3.93 mm.; a dark species, about as broad as long and broadest between the spiracular plates, where it is about 5 times as wide as the distance between the tips of the scapulae; numerous scattered, short, pale hairs.

Scutum.—Dark brown to black laterally and posteriorly, paler medianly with darker areas and lines and presenting, in general, a rugose appearance with depressions and sometimes raised smooth areas usually adjacent to festoons, which are well marked and furnished with strongly chitinous plates also ventrally; punctations very numerous and irregular, large punctations few and scattered medianly and posteriorly, more numerous laterally where some confluency occurs; marginal groove deep, conspicuous, and complete.

Capitulum.—Length 1.0-1.2 mm.; basis 0.63-0.66 mm. wide, its posterior border concave with shallow, rounded cornua, numerous small punctations dorsally; palpi 0.66 mm. long, article 2 about twice as long as article 3; hypostome dentition 4/4, the inner file of 10-12 very fine and delicate teeth, other files of 6-8 well-developed teeth.

Venter.—Pale, with festoons, anus, spiracular plates, and points of coxal spurs dark brown; a small rounded chitinous plate (plaque) immediately anterior to the median festoon, the fourth festoon on each side, and to the interval between the second and third festoons on each side, respectively (counting from the spiracular plate).

Spiracular plates.—Shape as in Figure 1*j*, 0.6-0.73 by 0.4-0.5 mm. with point extended dorsally.

Legs.—Pale and dark brown; coxa I with 2 strong, but short, subequal, blunt spurs, coxae II-IV each with 1 similar-type spur; tarsus I 0.8 mm. long, metatarsus about three-quarters the length of tarsus; tarsi II-IV about 1.0 mm. long, all tarsi with only moderate-sized humps, and with terminal spurs.

Female

Diagnosis

Body of unengorged female thickly clothed with decumbent hairs; scutum inornate, rugose with a conspicuous indentation of margin below lateral angle; porose areas subcircular or broadly oval; hypostome dentition usually 4/4, rarely 3/3; coxae as in male, tarsi humped but no apparent spurs.

Description

Body.—Size 4.3-12.9 by 4.0-10.7 mm.; pale with dark brownish scutum, capitulum, and legs; dorsum thickly clothed with decumbent pale hairs, which become scattered as engorgement proceeds.

Scutum.—Size 2.0-2.12 by 2.33-2.5 mm.; dark brown, frequently paler in the area enclosed by the cervical grooves and depressions and with a pale spot in the posterior angle (seen in only a few specimens and apparently readily lost when preserved in alcohol); postero-lateral margins slightly concave; punctations very numerous and irregular, giving the scutum a rugose appearance, particularly in the lateral and sometimes in the median fields, some confluency of large punctations laterally to form a conspicuous indentation of the scutal margin just below the lateral angle; cervical grooves continued to posterior margin by usually conspicuous and slightly divergent depressions, less obvious in very rugose scuta.

Capitulum.—Length 1.17-1.33 mm.; basis 0.83-0.93 mm. wide, the posterior margin somewhat concave, cornua rounded and not very obvious; porose areas large, subcircular or broadly oval, the interval somewhat depressed and slightly less than their transverse diameter; palpi 0.83-1.06 mm. long; hypostome dentition as in male though rarely the inner delicate file of teeth may be reduced to 3.

Spiracular plates.—Shape as in Figure 1*i*, 0.7-0.76 by 0.46 mm., with narrow point extended dorsally.

Legs.—Coxal spurs as in male; tarsus I 1.03 mm. long, tarsus IV 0.87 mm. long; all tarsi humped but not strongly so, most pronounced on tarsus I; tarsal spurs not apparent.

Hosts and Distribution

A. trachysauri appears to be a southern species, for the locality records, with the exception of a single record from Vaucluse, N.S.W., are confined to Victoria and South Australia. The hosts include the stumpy-tailed lizard, *Trachysaurus rugosus* Gray 1927, which appears to be the most common host, the southern blue-tongued lizard, *Tiliqua nigrolutea* Gray 1831, and the snakes *Denisonia superba* (Günther 1858) and *Notechis scutatus* var. *niger* (Kinghorn 1921). This tick has also been taken from a "blue-tongue" lizard and a "jew" lizard.

Comments

A. trachysauri was described by Lucas from specimens collected from *Trachysaurus scaber* in the Paris Museum. As no such species of *Trachysaurus* exists in Australia, some doubt has been expressed by Ferguson (1925) and others as to whether this tick is an Australian species. The descriptions given by Lucas (1861) and by Neumann (1899) fit the species determined as *A. trachysauri* by the writer very closely and it seems evident that *T. scaber* was erroneously recorded by Lucas for *T. rugosus*.

Tubb (1938) recorded *A. hydrosauri* (Denny) from *Tiliqua nigrolutea* Gray 1831, Mornington and Fern Tree Gully, Vic., and from *Trachysaurus rugosus* Gray 1827 and *Notechis scutatus* var. *nigar* Kinghorn 1921, the Sir Joseph Banks Is., Spencer Gulf, S.A. These hosts are those on which *A. trachysauri* occurs. Furthermore, as *A. hydrosauri* was considered by Neumann (1906) to be identical with *A. concolor*, which, in the extensive material studied by the writer, did not include any representatives of the Reptilia among its hosts, it seems evident that Tubb was dealing with *A. trachysauri*.

APONOMMA HYDROSAURI (Denny)

Plate 1, Figs. 1, 4; Fig. 2*a-i*

1843 *Ixodes hydrosauri* Denny, p. 314, fig. 4.
1844 *Amblyomma hydrosauri* (Denny), L. Koch, p. 231.
1899 *Aponomma hydrosauri* (Denny), Neumann, p. 197.
1899 *Aponomma concolor* Neumann, p. 198.
1900 *Aponomma hydrosauri* (Denny), Froggatt, p. 2.
1906 *Aponomma concolor* Neumann, Rainbow, p. 169.
1906 *Aponomma concolor* Neumann, p. 213.
1906 *Aponomma hydrosauri* (Denny), Neumann, p. 213.
1913 *Aponomma hydrosauri* (Denny), Patton and Cragg, p. 623.
1925 *Aponomma hydrosauri* (Denny), Ferguson, p. 34.
1926 *Aponomma hydrosauri* (Denny), Fielding, p. 87, fig. 33.
1947 *Aponomma hydrosauri* (Denny), Seddon, p. 29.
1947 *Aponomma hydrosauri* (Denny), Roberts, p. 11.

Larva unknown.

Nymph

Diagnosis

Scutum 0.50-0.57 by 0.70 mm., with relatively coarse punctations laterally and a small indentation of its margin below lateral angle; cervical groove with deep, strongly divergent depressions, which reach the scutal margin; hypostome dentition usually 2/2; tarsi humped but without spurs.

Description

Body.—Size 2.7-3.7 by 2.5-2.9 mm. (engorged specimens); very pale, almost whitish in colour, with widely scattered, very short, white hairs and very pale, brownish scutum and capitulum.

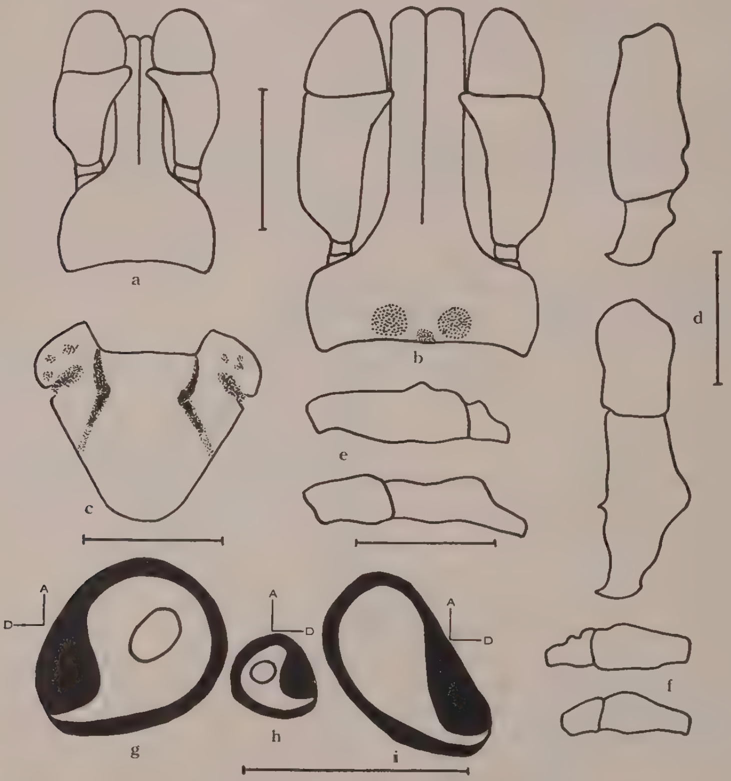

Fig. 2.—*Aponomma hydrosauri*. *a,* Capitulum of male (dorsal view); *b,* capitulum of female (dorsal view); *c,* scutum of nymph; *d,* tarsi I and IV of male; *e,* tarsi I and IV of female; *f,* tarsi I and IV of nymph; *g,* spiracular plate of female; *h,* spiracular plate of nymph; *i,* spiracular plate of male. The straight lines each represent 0.5 mm.

Scutum.—Size 0.50-0.57 by 0.70 mm.; much broader than long, very pale brown, sometimes with a darker spot below the lateral angles, posterior angle somewhat narrow and rounded, postero-lateral margins almost straight, at most only slightly concave; punctations few and very fine in median field, relatively coarse laterally, where some confluency occurs, the scutal margin with a small indentation below the lateral angle; cervical grooves continued posteriorly to the scutal margin by conspicuous and strongly divergent depressions.

Capitulum.—Length 0.47-0.5 mm.; basis 0.33-0.4 mm. wide, posterior margin straight, lateral margins slightly rounded; palpi slender, 0.27-0.33 mm. long, article 2 not much longer than article 3; hypostome dentition 2/2 of 5 or 6 teeth, sometimes an extra innermost file of 2 or 3 very small teeth.

Spiracular plate.—Shape as in Figure 2*h;* 0.17-0.2 by 0.17-0.2 mm.

Legs.—Coxal spurs as in male; tarsi humped and without spurs.

Male

Diagnosis

A medium-sized species; scutum inornate with numerous, uneven punctations; marginal groove complete, comparatively shallow to first festoon; hypostome dentition 3/3; coxa I with 2 subequal spurs, coxae II-IV each with 1 short spur; tarsi conspicuously humped, tarsus I with a single terminal spur, tarsi II-IV each bicalcarate.

Description

Body.—Size 2.4-2.7 by 2.2-2.5 mm., a little longer than broad, and broadest in the region of the spiracles.

Scutum.—Brownish, darker laterally and posteriorly, and with darker areas and streaks medianly; punctations numerous, uneven, most numerous and coarsest posteriorly and laterally; marginal groove complete, broad and comparatively shallow anterior to the first festoon; festoons well marked.

Capitulum.—Length 0.9-1.1 mm.; basis 0.6-0.7 mm. wide, posterior margin concave with broad, shallow, not very obvious cornua, lateral margins rounded, dorsal surface depressed medianly; palpi stout, 0.66 mm. long, article 2 with a conspicuous finger-like prolongation of its inner, anterior angle; hypostome dentition 3/3, the inner file of 9-12 very small and delicate teeth, other files of 5-7 much stouter teeth.

Spiracular plate.—Shape as in Figure 2*i,* 0.53 by 0.37 mm.

Legs.—Coxa I with 2 subequal stout spurs of medium length, coxae II-IV each with a single similar spur; tarsi all conspicuously humped, tarsus I with a single terminal spur, other tarsi with 2 spurs.

Female

Diagnosis

A large tick when fully engorged; scutum at least 1.7 mm. long, slightly broader than long, inornate, with numerous uneven punctations, mainly coarse laterally and with a short indentation of the margin below the lateral angle; porose areas small, deep, and circular or subcircular; hypostome dentition, coxae, and tarsi as in the male, but no spurs on tarsi.

Description

Body.—Size 4.4-11.1 by 4.0-11.4 mm.; dorsum usually pale with scattered, very small, pale hairs.

Scutum.—Size 1.7-2.1 by 1.8-2.4 mm., slightly broader than long, usually dark brown, the median area paler, the posterior angle relatively narrow, the postero-lateral margins concave; punctations numerous and somewhat uneven, the larger punctations spaced and distributed mainly laterally, a short but conspicuous indentation of the scutal margin immediately posterior to the lateral angle, and frequently in line with 1 or 2 large punctations in the lateral field; cervical grooves continuing posteriorly into shallow, ill-defined, slightly divergent depressions.

Capitulum.—Length 1.1-1.33 mm. long; basis 0.9-1.0 mm. wide, the posterior margin concave but without distinct cornua; porose areas relatively small, deep, circular or subcircular, the interval about as wide as their diameter; hypostome dentition as in the male.

Spiracular plate.—Shape as in Figure 2*g*; 0.63-0.78 by 0.5 mm.

Legs.—Comparatively short and slender; coxal spurs as in the male; tarsus I 0.78 mm., metatarsus 0.55 mm. long, tarsus IV of similar length, all tarsi with conspicuous humps and without spurs.

Hosts and Distribution

Froggatt (1900) reported *A. hydrosauri* as "our common lizard tick." No reptiles of any species were included among the hosts of the material examined by the writer, the hosts being the horse, ox, spiny ant-eater (*Tachyglossus* sp., and *T. aculeatus* Shaw & Nodder 1792), and the bandicoot (*Perameles* sp.). This tick appears to be most common on the spiny ant-eater.

A. hydrosauri is recorded from Queensland, New South Wales, and Victoria. It has a wide distribution in Queensland, occurring throughout the coastal areas from Dunk I. to Brisbane. The New South Wales records include Sydney, Goulburn, and Bombala. In Victoria, it has been taken at Dromana and Melbourne.

Comments

The species *A. hydrosauri* was described by Denny (1843) from a female taken from *Varanus* (*Hydrosaurus*) *gouldii* (Shaw 1790). The name *A. concolor* was given by Neumann (1899) to a male from a species of *Tachyglossus* ("*Hystrix*"). Neumann (1906) subsequently saw the female of *A. concolor* and decided that *A. concolor* and *A. hydrosauri* were synonymous.

The male of the species described by the author under the name *A. hydrosauri* agrees very closely with Neumann's description of *A. concolor.* There is some doubt, however, of the synonymy of this species with Denny's *A. hydrosauri.* The hypostome dentition of *A. concolor* was recorded by Neumann as 3/3 and that of *A. hydrosauri* by Denny as 4/4. Furthermore, the host of *A. hydrosauri* was noted by Denny as a species of Reptilia and that of *A. concolor* by Neumann as a species of spiny ant-eater ("*Hystrix*"). The material examined by the author originated almost exclusively from the spiny ant-eater; certainly no reptilian hosts were present.

It seems therefore that Denny's *A. hydrosauri* has stronger claims for synonymy with *A. trachysauri* than with *A. concolor,* but, until Denny's type material can be examined, it is considered advisable to permit Neumann's decision to stand.

APONOMMA AURUGINANS Schultz

Plate 2, Figs 1, 3; Fig. 3*a-g*

1936 *Aponomma auruginans* Schultz, p. 625, figs. 6-8.
1946 *Aponomma auruginans* Schultz, Taylor, p. 125.

Larva unknown.

Nymph

Diagnosis

Scutum 0.7-0.75 by 0.73-0.8 mm., punctations few and inconspicuous, an indentation of the margin below the lateral angle; basis capituli with cornua; hypostome dentition 2/2; coxal spurs as in female; tarsi strongly humped but without spurs.

Description

Body.—Size 2.43-3.0 by 1.9-2.33 mm., longer than broad, pale with scattered, short, pale hairs and brownish scutum and capitulum.

Scutum.—Size 0.7-0.75 by 0.73-0.8 mm., about as long as wide; posterior angle broad and rounded, postero-lateral margins straight or, at most, only very slightly concave; punctations few and inconspicuous, except in lateral fields where some confluency occurs to form an indentation of the margin below the lateral angle; cervical grooves deep, convergent, continued posteriorly by deep, narrow, divergent depressions, which shallow perceptibly before reaching the scutal margin.

Capitulum.—Length 0.5 mm.; basis 0.33 mm. wide, posterior margin concave with obvious cornua; palpi 0.37 mm. long, article 2 about 1½ times article 3; hypostome dentition 2/2.

Spiracular plate.—Shape as in Figure 3*g;* 0.2 by 0.17 mm.

Legs.—Coxal spurs as in female, coxa I prolonged anteriorly as in female; tarsi stout, strongly humped, no spurs.

Male

Diagnosis

An *Amblyomma*-like species; scutum inornate; relatively smooth; marginal groove ill defined and incomplete; basis capituli with conspicuous cornua; hypostome dentition 2/2; coxa I with conspicuous anterior prolongation and with 2 short, subequal spurs, coxae II-IV each with a single spur; tarsi strongly humped, their tips bifid dorsally, no spurs.

Description

Body.—Size 2.8-3.1 by 2.54-2.56 mm., longer than broad, brown, darker in region of festoons, which are well marked.

Scutum.—Punctations relatively few, fine and scattered, and almost absent medianly, a series of slightly coarser punctations posteriorly and laterally in the region of the marginal groove; marginal groove short, shallow, ill defined, and incomplete, extending only to anterior festoons and represented anteriorly by a few coarse punctations.

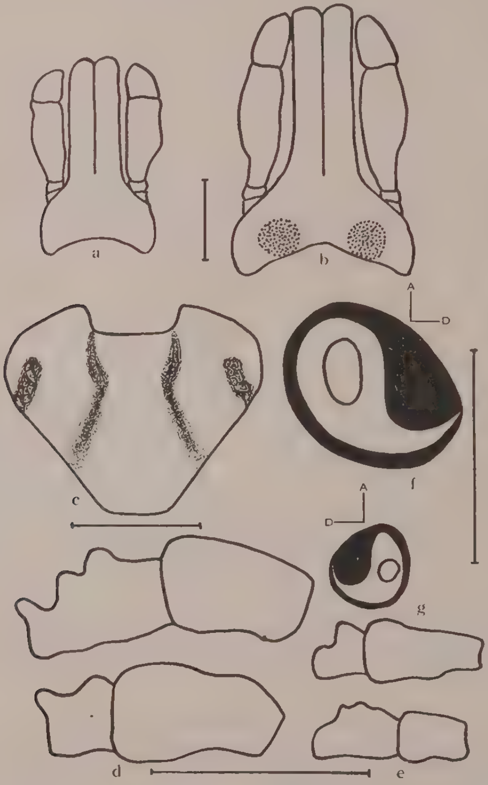

Fig. 3.—*Aponomma auruginans.* *a,* Capitulum of male (dorsal view); *b,* capitulum of female (dorsal view); *c,* scutum of nymph; *d,* tarsi IV and I of male; *e,* tarsi I and IV of nymph; *f,* spiracular plate of female; *g,* spiracular plate of nymph. The straight lines each represent 0.5 mm.

Capitulum.—Length 0.7-0.83 mm.; basis 0.53 mm. wide, posterior margin concave with well-marked cornua, lateral margins slightly rounded; palpi 0.53 mm. long; hypostome dentition usually 2/2, as in the female.

Spiracular plate.—Shape as in Figure 3*f*, 0.47 by 0.3 mm., with a conspicuous dorsal prolongation.

Legs.—Coxae and tarsi as in the female.

Female

Diagnosis

A medium-sized species; scutum about as long as broad, inornate, with fine punctations medianly, but more rugose laterally and an indentation of its margin immediately below the lateral angle; basis capituli with a conspicuous median indentation on its posterior border and with well-developed cornua; porose areas large, circular, touching posterior margin of basis capituli; hypostome dentition, coxae, and tarsi as in male.

Description

Body.—Size 5.6-9.3 by 4.5-6.3 mm. (semi-engorged and engorged specimens), longer than broad, spirit specimens greyish yellow with brownish scutum and capitulum and scattered, short, pale hairs.

Scutum.—Size 1.6-1.9 by 1.6-1.8 mm., about as long as broad; brownish, paler medianly; posterior angle fairly broad, postero-lateral margins straight or slightly concave; punctations numerous, uneven, mainly moderately fine and well distributed in the median and posterior fields, larger and more rugose laterally, a conspicuous, elongate indentation of large, confluent punctations from the scutal margin just below the lateral angle; cervical grooves very deep with some rugosity near their inner margin, continuing posteriorly as slightly divergent depressions, which become obscure as they approach the scutal margin.

Capitulum.—Length 1.07-1.1 mm.; basis 0.8 mm. wide, the posterior margin markedly concave, with a broad median indentation and conspicuous cornua, lateral margins rounded; porose areas large, circular, and shallow encroaching on the posterior margin, the interval at least equal to their diameter; palpi 0.77-0.87 mm. long, article 2 about 1½ times as long as article 3; hypostome dentition 2/2 of 5-7 teeth, with sometimes 1 or 2 very fine teeth present as an extra and inner file.

Spiracular plate.—Shape as in Figure 3*f*; 0.53 by 0.4 mm. with a dorsal prolongation.

Legs.—Coxa I with a conspicuous, anteriorly pointed prolongation and with 2 subequal, stout, blunt spurs of moderate length; coxae II-IV each with a single similar spur; tarsi without spurs, stout and strongly humped, their tips being bifid dorsally into 2 flaps, which are directed forwards.

Hosts and Distribution

A. auruginans appears to be confined to the wombat, and, in the collections examined, the host is given as *Vombatus hirsutus* Perry 1810 (*Phascolomys mitchelli*), *Vombatus* sp. (*Phascolomys* sp.), wombat, and Victorian wombat. The locality records include Mittagong, Glenfield, Sydney, Cooma, Wee Jasper, and Mudgee in New South Wales and Melbourne in Victoria. The Melbourne record is from the Veterinary Research Institute and probably refers to a specimen forwarded there for identification from some other part of Victoria.

Aponomma tachyglossi, sp. nov.

Plate 2, Fig. 4; Fig. *4a-d*

Male and nymph unknown.

Female

Holotype.—Female (engorged), from Wowan, Queensland, 10.vi.1937 (J. W. Mackay). Host, *Tachyglossus aculeatus* Shaw & Nodder 1792. In the Queensland Museum, Brisbane.

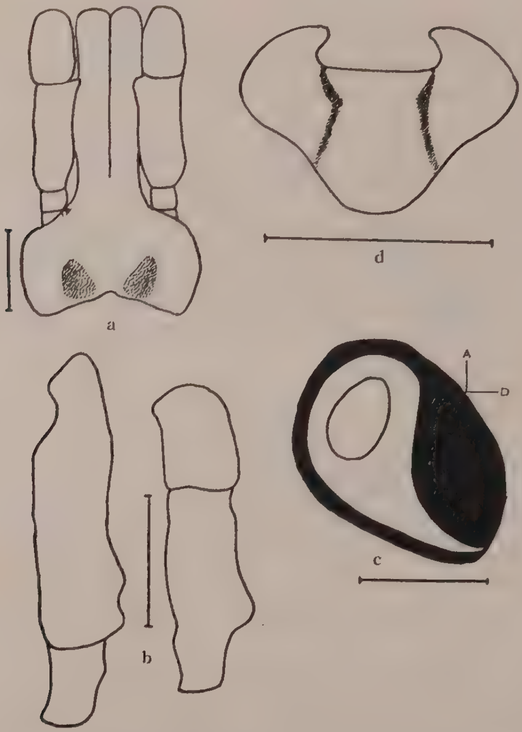

Fig. 4.—*Aponomma tachyglossi. a,* Capitulum of female (dorsal view); *d,* tarsi I and IV of female; *c,* spiracular plate of female; *d,* scutum of larva. The straight lines each represent 0.5 mm.

Paratypes.—From *Bos taurus* (Linn. 1758), Degilbo, Queensland, 14.x.1937 (F. Goodchild), 1 ♀; from *Tachyglossus* sp., Boomba, Queensland, 2.viii.1948, 3 ♀; host? Monto, Queensland, 8.vi.1943 (P. K. Smith), 1 ♀. The paratypes from Degilbo and Boomba are in the collection of the Animal Health Station, Department of Agriculture and Stock, Yeerongpilly, Queensland, and that from Monto in the collection of the Queensland Museum.

Diagnosis

A large tick when engorged; scutum broader than long, inornate, and with a deep indentation of its margin below the lateral angle; porose areas large, deep, triangular, a broad, shallow V-shaped depression on basis capituli anterior to porose areas; hypostome dentition 4/4; coxa I with 2 spurs, coxae II-IV each with 1 spur; trochanters with a broad, ridge-like, but not very obvious spur; tarsi with terminal spurs.

Description

Body.—Length 19.3 mm., greatest width 15.7 mm., broadly oval and widest in mid-body region; dorsum with very short, evenly distributed, pale hairs.

Scutum.—Wider than long (2.6 by 3.07 mm.), dark brown in the lateral and scapular fields, lighter brown in the median and posterior fields; posterior angle relatively narrow, postero-lateral margins slightly concave; punctations uneven and irregularly distributed, mainly fine medianly and anteriorly, coarser laterally where some confluency occurs to form a deep and well-marked indentation of the scutal margin just below the lateral angle; cervical grooves deep and convergent, continuing posteriorly into shallow but prominent and slightly divergent depressions, which attain the posterior margins.

Capitulum.—Length 2.0 mm.; basis 1.27 mm. wide, the posterior margin concave and with a median indentation, the lateral margins rounded; porose areas large, deep, subtriangular, their apices divergent anteriorly, the interval increasing in width anteriorly, its narrowest width not quite equal to the width of the base of the porose areas; a broad, shallow, V-shaped depression anterior to the porose areas; palpi 1.33 mm. long; article 3 being 0.4 mm. long and about half the length of article 2; hypostome dentition 4/4, the inner file of 10-12 very fine teeth, the other files of 7-9 much stouter teeth.

Genital opening.—Opposite coxa II.

Legs.—Stout and strong with pale joints; coxa I with 2 stout, subequal spurs of moderate length, coxae II-IV each with a single stout, similar spur on its outer angle; trochanters each with a single broad, shallow, ridge-like, and not very obvious ventral spur, most prominent on trochanter IV; tarsus I 1.4 mm. long, the metatarsus 1.0 mm. long, tarsus IV 0.97 mm. long, the metatarsus 0.23 mm., tarsal humps present and strongest on tarsus IV; terminal spurs present but not very obvious.

Spiracular plate.—Shape as in Figure 4*c*, greatest dimensions 0.83 by 0.67 mm.

Larva

Morphotype.—Larva bred from paratype female from Boompa, Queensland; in the Queensland Museum.

Diagnosis

Scutum 0.35 by 0.54 mm., no obvious punctations; hypostome dentition 2/2; coxa I with 2 subequal, small spurs, coxae II-IV each with a single spur; tarsus I with slight hump.

Description

Body.—Length 0.81 mm., greatest width 0.79 mm.; subcircular; festoons well marked.

Scutum.—Much broader than long (0.34 by 0.54 mm.); posterior and lateral angles broad and rounded, postero-lateral margins concave; no obvious punctations; cervical grooves continued posteriorly by conspicuous divergent depressions.

Capitulum.—Length 0.29 mm.; basis subtriangular, 0.19 mm. wide; palpi 0.18 mm. long, article 3 a little more than half the length of article 2; hypostome dentition 2/2, the inner file of up to 4 strong teeth, the outer file of up to 6 teeth.

Legs.—Coxa I with 2 subequal, small spurs, other coxae each with 1 similar spur; tarsus I 0.28 mm. long, tarsus III 0.2 mm. long, slight boss on tarsus I, other tarsi not bossed, tarsal spurs absent.

Comments

The female paratypes show remarkably little variation from the holotype. Body measurements range from 5.75 to 29.3 by 4.5 to 15.7 mm.; length of the capitulum from 1.1 to 2.0 mm.; length of the palpi from 0.8 to 1.33 mm.; and scutal measurements from 1.5 to 2.6 by 2.1 to 3.07 mm.

The species is erroneously listed by Roberts (1947) and by Seddon (1947) as *A. trachysauri* from cattle.

APONOMMA TROPICUM, sp. nov.

Plate 2, Fig. 2; Fig. 5*a-d*

Male, nymph, and larvae unknown.

Female

Holotype.—Female from Dunk I., Queensland, 25.viii.36 (H. Brassey). Host, "Albino Echidna." In the Queensland Museum (W 6.71).

Paratypes.—Twenty-one females, Dunk I., Queensland, 16.x.36 (H. Brassey) from "Albino Echidna." In the Queensland Museum.

Diagnosis

A moderate-sized tick closely resembling *A. hydrosauri;* scutum at most 1.6 mm. long, inornate; capitulum 1.0 mm. long; the posterior border of basis capituli concave with a median indentation; porose areas deep, subcircular, almost reaching posterior border of basis capituli; hypostome dentition 3/3.

Description

Body.—An engorged specimen, about 8.1 by 8.2 mm., subcircular in shape, pale with darker scutum and capitulum and with sparse, short, delicate hairs; dorsal and ventral grooves, except anal groove, not obvious; festoons inapparent.

Scutum.—Triangular in shape, wider than long (1.5 by 1.78 mm.), posterior angle relatively narrow and rounded, postero-lateral margins concave; punctations numerous, uneven, fine mainly in posterior field, coarser elsewhere, particularly laterally, where some confluency occurs to form a moderate indentation of the postero-lateral margin below the lateral angle; cervical grooves short, deep, and convergent, continued posteriorly by 2 well-defined, divergent depressions, which reach the posterior border.

Capitulum.—Length 1.0 mm.; basis 0.8 mm. wide, posterior border depressed and concave with a central indentation, the postero-lateral angles swollen, rounded, and slightly prominent, lateral sides rounded; palpi 0.66 mm. long; article 3 0.23 mm. long, slightly more than half the length of article 2, porose areas deep, relatively large, subcircular, almost encroaching on the posterior border of the basis capituli, the interval less than their diameter; hypostome dentition 3/3, the inner file consisting of small, delicate teeth, other files of 5-7 stouter teeth.

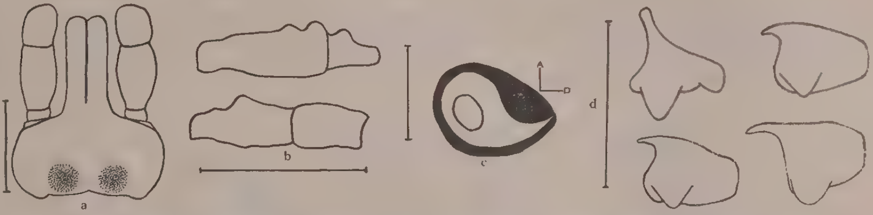

Fig. 5.—*Aponomma tropicum* (female). *a*, Capitulum (dorsal view); *b*, tarsi I and IV; *c*, spiracular plate; *d*, coxae I-IV. The straight lines each represent 0.5 mm.

Legs.—Relatively small and slender; coxa I with 2 subequal moderate but stout, blunt spurs, coxae II-IV each with a single similar spur on the exterior angle; trochanters each with a faintly visible, ventral, ridge-like spur, most obvious on trochanter IV; tarsi humped and without spurs, tarsus I 0.53 mm. long, metatarsus 0.37 mm., tarsus IV 0.5 mm. long, metatarsus 0.20 mm.

Spiracular plate.—Shape as in Figure 5*c*, the greatest dimensions 0.56 by 0.4 mm.

Comments

There appears to be little variation from the holotype among the paratype specimens except in measurements. These are:

Body dimensions, 5.3-12.3 by 5.0-11.8 mm.; scutum, 1.33-1.56 by 1.50-1.78 mm.; capitulum, 0.83-1.0 mm.; basis width 0.73-0.80 mm.; palpi, 0.63-0.68 mm. long.

This species bears a close resemblance to *A. hydrosauri,* from which it differs in possessing a smaller scutum (*A. tropicum* 1.33-1.56 by 1.50-1.78 mm. and *A. hydrosauri* 1.7-2.1 by 1.8-2.5 mm.) and a smaller capitulum (0.83-1.0, *A. tropicum,* and 1.1-1.32, *A. concolor*). There is also a difference in the size and appearance of the basis capituli and of the porose areas.

Among the paratype material and from the same host was a single typical female *A. hydrosauri,* evidence that *A. tropicum* is not a northern form or variety of *A. hydrosauri.*

APONOMMA DECOROSUM (L. Koch)

Plate 3, Figs. 1, 3; Fig. 6*a-f*

1867 *Ixodes decorosus* L. Koch, p. 241.
1867 *Ixodes varani* L. Koch, p. 241.
1899 *Aponomma decorasum* (L. Koch), Neumann, p. 194, figs. 46-7.
1900 *Aponomma decorosum* (L. Koch), Froggatt, p. 2.
1906 *Aponomma decorosum* (L. Koch), Rainbow, p. 168.
1913 *Aponomma decorosum* (L. Koch), Patton and Cragg, p. 263.
1925 *Aponomma decorosum* (L. Koch), Ferguson, p. 34.
1826 *Aponomma decorosum* (L. Koch), Fielding, p. 89, fig. 35.
1934 *Aponomma decorosum* (L. Koch), McIntosh, p. 21.

Larva unknown.

Nymph

Diagnosis

Scutum 0.62 by 0.8 mm., large punctations with some confluency in lateral fields with sometimes an indentation of the margin below the lateral angles; hypostome dentition 2/2 of 5 or 6 teeth; coxa I with 2 small, subequal spurs, other coxae each with 1 spur.

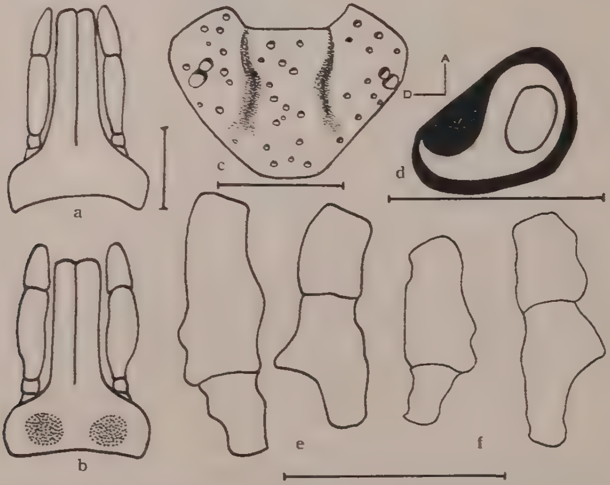

Fig. 6.—*Aponomma decorosum.* *a*, Capitulum of male (dorsal view); *b*, capitulum of female (dorsal view); *c*, scutum of nymph; *d*, spiracular plate of male; *e*, tarsi I and IV of female; *f*, tarsi I and IV of male. The straight lines each represent 0.5 mm.

Description

Body.—Almost circular, 1.75 by 1.7 mm., pale, with brownish scutum and capitulum, dorsum with scattered, very short, pale hairs.

Scutum.—Size 0.62 by 0.8 mm., broader than long, postero-lateral margins straight or slightly convex; brown with darker lateral fields; some relatively large, scattered punctations with some confluency in the lateral fields forming deep depressions, which may attain the margin; cervical grooves continued posteriorly by deep depressions, which broaden and become shallow and divergent, but do not quite attain the posterior scutal margin.

Capitulum.—Length 0.38 mm.; basis 0.30 mm. wide with slight cornua; palpi 0.25 mm. long, article 2 a little longer than article 3; hypostome dentition 2/2 of 5 or 6 teeth in each file.

Spiracular plate.—Oval in shape, 0.15 by 0.10 mm.

Legs.—Coxa I with 2 small, subequal, blunt spurs, other coxae each with 1 similar spur; tarsi humped but not spurred.

Male

Diagnosis

A small, circular tick with conspicuous brownish red and white coloration; marginal groove well marked but incomplete; coxae as in nymph; tarsi strongly humped and with slight terminal spurs.

Description

Body.—An ornate species with reddish brown and white coloration, almost circular in shape; 1.5-2.3 by 1.4-2.7 mm.

Scutum.—Reddish brown, encircled laterally and posteriorly with whitish coloration and with a broad, median, inverted Y-shaped, whitish area; punctations numerous, uneven, most numerous laterally and posteriorly, the coarsest punctations being immediately anterior to the festoons and also towards the scapulae where they are sometimes confluent and extend the marginal groove anteriorly; marginal groove deep, conspicuous but incomplete, extending only as far as first festoon, though frequently represented posteriorly by a series of large but separate punctations.

Capitulum.—Length 0.9 mm.; basis 0.83-0.93 mm. wide, sometimes provided dorsally with shallow linear markings and sometimes with an irregular series of small punctations; palpi 0.5-0.53 mm. long, article 2 about 1½ times as long as article 3; hypostome dentition 3/3, an inner file of 10-12 very fine teeth, other files of 6-8 much stouter teeth.

Spiracular plate.—Shape as in Figure 6*d*, 0.33 by 0.2 mm.

Legs.—Coxa I with 2 short, broad, subequal spurs, coxae II-IV each with 1 similar spur; tarsus I strongly humped, with a slight terminal spur, tarsi II-IV also strongly humped and also with slight terminal spurs.

Female

Diagnosis

A small tick; scutum cordate, slightly broader than long, brownish red with a large, white median marking, punctations numerous, coarser and confluent laterally; porose areas relatively large, circular or subcircular; hypostome dentition 3/3; tarsi humped but without spurs.

Description

Body.—Size 2.53-4.8 by 2.3-3.9 mm., longer than broad and broadest in the region of the posterior half to posterior third, dorsum dark with numerous evenly distributed, very short but stout, pale hairs.

Scutum.—Size 1.3-1.8 by 1.5-1.9 mm., slightly broader than long, the posterior angle very broad and rounded, the postero-lateral margins almost straight, sometimes slightly concave; brownish red with whitish coloration occupying the area between the cervical grooves and extending posteriorly for about half the length of the scutum; punctations numerous, uneven, mainly large, fairly evenly distributed, coarser and confluent in lateral fields, sometimes forming a conspicuous and elongate indentation of the margin immediately below the lateral angle; cervical grooves continued posteriorly by rather broad, shallow, slightly divergent depressions, which do not reach the scutal margin.

Capitulum.—Length 0.76-0.93 mm.; basis swollen at base of hypostome and along lateral margins, posterior margin slightly concave, lateral margins convex; porose areas relatively large, circular or subcircular, interval less than diameter; palpi 0.57-0.61 mm. long; hypostome dentition 3/3, teeth as in the male.

Spiracular plate.—Shape as in Figure 6*d*, 0.35-0.41 by 0.23-0.27 mm.

Legs.—Coxae as in the male; tarsi I 0.55 mm. long, moderately humped, tarsi II-IV 0.43-0.45 mm. long, strongly humped, no tarsal spurs.

Hosts and Distribution

This species is recorded from many localities in Queensland, extending from Townsville in the north to Coolangatta in the south and as far west as Goondiwindi. It also occurs in New South Wales, where it is recorded from Sydney, Chichester, Myall Lakes, and Jerilderie. It is apparently unknown in other States. The material examined was, with one exception, collected from *Varanus varius* Shaw 1790, *Varanus* sp., or "Goanna." The exception was from a "bluetongue lizard."

Neumann (1899) also records *A. decorosum* from Fiji.

Comments

This is a very distinct and readily recognized species. The rich reddish brown colour of the scutum may in time lose its identity in spirit specimens, but the whitish ornamentation, in both sexes, may still be apparent in specimens up to 50 years old.

APONOMMA SIMPLEX Cooper and Robinson

Plate 3, Figs. 2, 4; Fig. 7*a-h*

1906 *Aponomma trimaculatum* Lucas, Rainbow, p. 168.
1908 *Aponomma simplex* Cooper and Robinson, p. 466, figs. 18-21.
1947 *Aponomma gervaisi* Lucas, Seddon, p. 29.

Nymph

Diagnosis

Scutum 0.66-0.73 by 0.8-0.9 mm., postero-lateral margins straight or slightly convex, several, large, scattered punctations and a few small ones; cervical grooves ending in short, ill-defined depressions; hypostome dentition 3/3; coxae each with a single short spur; tarsi humped but without spurs.

Description

Body.—Size 1.2-1.9 by 1.1-1.6 mm.; dorsum with many pits less obvious in engorged specimens and with scattered, delicate, short, pale hairs; festoons conspicuous, but less apparent as engorgement proceeds.

Scutum.—Brownish, 0.66-0.73 by 0.8-0.9 mm., broader than long, the posterior and lateral angles broad and rounded, the postero-lateral margins almost straight, at most very slightly concave; several large, scattered punctations and a few small ones; cervical grooves followed by short, ill-defined, broad, shallow depressions.

Capitulum.—Length 0.40-0.45 mm.; basis 0.25 mm. long, posterior border straight; hypostome dentition 3/3 of 5-9 teeth; palpi 0.25 mm. long, articles 2 and 3 subequal.

Spiracular plate.—Shape as in Figure 7*h*, 0.17 by 0.12 mm.

Legs.—Coxae each with a single not very obvious, short spur; tarsus I 0.25 mm. long, metatarsus 0.12 mm. long, tarsus IV 0.27 mm. long, metatarsus 0.17 mm. long, all tarsi with well-developed humps but no spurs.

Male

Diagnosis

A small tick, 2-2.7 mm. long, subcircular, ornate with 5 iridescent, green markings, the lateral markings usually curved inwardly at their posterior extremities; marginal groove absent; hypostome dentition 4/4; coxae as in the nymph; tarsus I with a single terminal spur, other tarsi bicalcarate.

Description

Body.—Size 2.0-2.7 by 1.9-2.7 mm., subcircular and widest in vicinity of spiracular plate.

Scutum.—Brown with 5 iridescent, green markings, namely a small median mark, a pair of elongate and irregular markings laterally, the posterior extremity being frequently extended internally, and a pair of small, square, triangular, or curved markings posteriorly and on either side of the median longitudinal line; punctations uneven and very numerous, most dense in lateral and posterior fields where the coarser punctations are most frequent; no marginal groove.

Capitulum.—Length 0.80-1.1 mm.; basis 0.5-0.6 mm. wide, the posterior margin very slightly concave, the lateral margins convex and the median dorsal field somewhat punctate; palpi 0.5-0.55 mm., article 2 not quite twice the length of article 3; hypostome dentition 4/4 of 8-10 teeth, the inner file small and delicate.

Spiracular plate.—Shape as in Figure 7g, 0.4-0.5 by 0.2-0.23 mm.

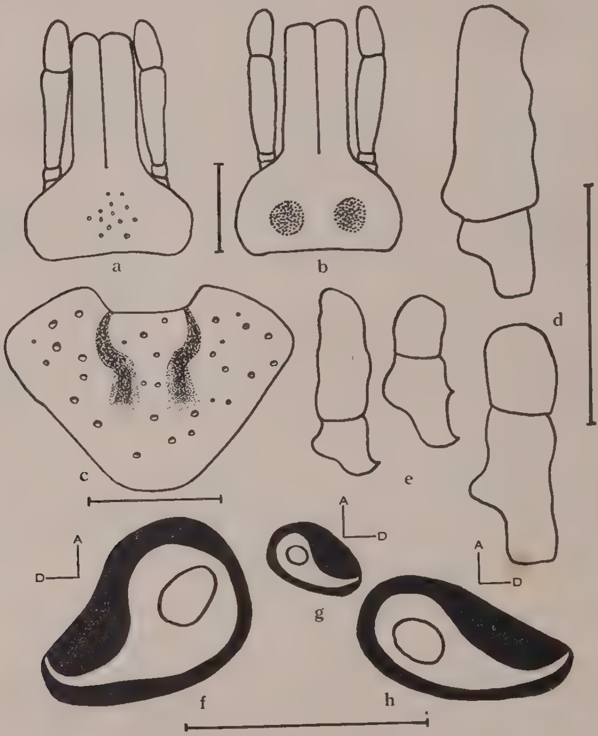

Fig. 7.—*Aponomma simplex.* *a,* Capitulum of male (dorsal view); *b,* capitulum of female (dorsal view); *c,* scutum of nymph; *d,* tarsi I and IV of female; *e,* tarsi I and IV of male; *f,* spiracular plate of female; *g,* spiracular plate of male; *h,* spiracular plate of nymph. The straight lines each represent 0.5 mm.

Legs.—Coxae each with 1 short, blunt spur, most prominent on coxa I; tarsi with prominent humps, bicalcarate except for tarsus I, which carries a single terminal spur.

Female

Diagnosis

A small species, the scutum broader than long and with 3 iridescent, green markings, the medium one large; porose areas deep and subcircular; hypostome dentition and coxae as in male; no tarsal spurs.

Description

Body.—Size 2.5-5.5 by 2.1-4.4 mm., dark, longer than broad, particularly as engorgement proceeds, and with short, but relatively stout, pale hairs scattered over the dorsum.

Scutum.—Broader than long, 1.3-1.8 by 1.6-2.0 mm., lateral and posterior angles very broad and rounded, the postero-lateral margins very slightly concave; 3 prominent, large, iridescent, greenish markings, 1 in each scapular field and 1 median, sometimes confluent in the region of the cervical grooves; punctations numerous, uneven, mainly large, fairly evenly distributed; cervical grooves succeeded by short, shallow, slightly divergent depressions, which do not extend far into the posterior half of the scutum.

Capitulum.—Length 0.9-1.0 mm.; basis 0.65-0.7 mm. wide, posterior margin straight; porose areas deep, subcircular, the interval about equal to their diameters; palpi 0.53-0.6 mm. long; hypostome dentition as in the male.

Spiracular plate.—Shape as in Figure 7*f*, 0.40-0.50 by 0.2-0.22 mm.

Legs.—Well developed and moderately strong; coxae as in the male, but spurs on coxae II-IV less obvious; tarsi humped and without spurs.

Hosts and Distribution

A. simplex appears to be the most common tick on snakes and the "goanna" in Australia. It is recorded in all States except Tasmania, and apparently reaches its highest development in Queensland and New South Wales. Table 1 gives the hosts and localities of the material studied. It will be noted that this species has been also taken from the ox and the horse.

COMMENTS

A. simplex was described by Cooper and Robinson (1908) from a single male tick from an "iguana" from Quamborne, N.S.W. The description of the male *A. simplex* given by the writer fits that of Cooper and Robinson very closely, but differs in one respect. In their description, the latter authors refer to the ornation of the male as being confined to "an indistinct greenish iridescent patch on either side." In the writer's description reference is made to 5 colour markings.

The material examined by the writer was very extensive and contained specimens in which the 5 green markings were distinct, specimens in which some of the markings had disappeared, and specimens in which no markings whatsoever could be detected. Undoubtedly, the spirit in which these specimens had been preserved was responsible for this deterioration in the colour pattern.

The *A. simplex* material in the collection of the Animal Health Station, Yeerongpilly, had been identified by the British Museum as *A. gervaisi* (Lucas). This tick has a very similar colour pattern to *A. simplex*, but its hypostome dentition is 3/3.

TABLE 1

HOSTS AND DISTRIBUTION OF *A. SIMPLEX*

State	Locality	Host
Queensland	Cape York	*Oxyranus scutellatus* Peters 1867
	Townsville	*Aspidites melanocephalus* Krafft 1864
	Townsville	Cattle
	Rockhampton	*Varanus varius* (Shaw 1790)
	Cairns	*Varanus* sp.
	Meringa	*Varanus* sp.
	Brisbane	Carpet snake
	Brisbane	*Varanus varius* (Shaw 1790)
	Ipswich	Horse
	Bondoola	*Varanus varius* (Shaw 1790)
	Bundaberg	"Black snake"
	Toowoomba	*Varanus* sp.
	Burpengary	*Varanus* sp.
	Dirranbandi	*Varanus* sp.
	Charleville	*Varanus* sp.
New South Wales	Picton Vale	"Black snake"
	Graman	"Goanna"
	Grafton	*Pseudechis porphyriacus* (Shaw 1794)
	Hornsby	*Varanus varius* (Shaw 1790)
	Quamborne	"Iguana"
	Gravesend	*Varanus varius* (Shaw 1790)
Victoria	Goulburn	"Tiger snake"
	Altona	*Demansia textilis* (Dumeril & Bidron 1854)
	Melbourne	"Black snake"
	Melbourne	*Pseudechis porphyriacus* (Shaw 1794)
Western Australia	———	*Demansia* sp.
	Perth	*Demansia textilis* (Dumeril & Bidron 1854)
South Australia	Purnong	"Brown snake"
Northern Territory	———	*Aspidites melanocephalus* Krafft 1864

APONOMMA ECINCTUM Neumann

1901 *Aponomma ecinctum* Neumann, p. 293.
1904 *Aponomma ecinctum* Neumann, Neumann, p. 234.
1906 *Aponomma ecinctum* Neumann, Rainbow, p. 169.
1908 *Aponomma ecinctum* Neumann, Cooper and Robinson, p. 470.
1911 *Aponomma ecinctum* Neumann, Neumann, p. 113.
1913 *Aponomma ecinctum* Neumann, Patton and Cragg, p. 623.
1925 *Aponomma ecinctum* Neumann, Ferguson, p. 34.
1926 *Aponomma ecinctum* Neumann, Fielding, p. 92.
1950 *Aponomma ecinctum* Neumann, Kohls, p. 25.

This species was described by Neumann from specimens forwarded by W. W. Froggatt, Sydney, and stated to have been collected from a lamellicorn beetle, *Aulacocyclus kaupi* Much. Neumann (1904) later recorded it on an Australian snake, *Diemenia superciliosa* (Spin. 1894) (erroneously cited by Neumann as a species of the Hemiptera : Insecta). In 1911, Neumann reported *A. ecinctum* from the Philippine Is. and Samoa from the snake *Engryus* *samoensis* and the lizard *Hydrosaurus giganteus.* Kohls (1950) included it in the list of Ixodoidea recorded from the Philippine Is., but did not encounter it in the material examined by him.

Neumann's description of *A. ecinctum* could quite readily refer to specimens identified by the writer as *A. simplex* and from which the green, iridescent markings have disappeared. These two names are, therefore, possibly synonymic, in which case the name *A. ecinctum* would have precedence over *A. simplex.* If this synonymy is correct, then the occurrence of *A. ecinctum* on an insect would be accidental. The writer feels, however, that the evidence for this conclusion is not as yet sufficiently convincing, particularly in view of Froggatt's statement (Neumann 1904) that the tick is very commonly found on the beetle from which the original specimens were collected.

APONOMMA QUADRATUM Cooper and Robinson

1908 *Aponomma quadratum* Cooper and Robinson, p. 468, figs. 22-24.
1945 *Aponomma quadratum* Cooper and Robinson, Theiler, p. 175.

This species was described by Cooper and Robinson from a single male taken from an "iguana" at Quamborne, N.S.W. No tick answering to this description has been seen by the writer. Cooper and Robinson's description is given below:

"Male, L. 2.6 mm., W. 2.8 mm. Body somewhat quadriform, wider behind than in front, broader than long. Scutum glabrous, punctate; dark-brown in centre, reddish-brown near margins; no metallic spots; punctations irregular, few coarse, many fine; cervical grooves short, deep, wide, straight and parallel; marginal grooves very indistinct; festoons well marked, small, broader than long; nine shallow symmetrically disposed depressions on posterior half of scutum. Venter pale greyish-yellow, scattered with numerous whitish hairs; genital orifice between coxae II; spiracles large, ear-shaped, with short tail running round to dorsum. Capitulum 1.1 mm., basis capituli trapezoidal, cornua very short and blunt; palps short; hypostome with small corona of minute teeth, not emarginate at tip, dentition 3/3. Legs of moderate size, coxae spurred; coxa I with a pair of short blunt spurs of which the internal is the longer; coxae II, III, and IV each with a single short blunt spur; tarsi bicalcarate, sharply attenuated near extremity; slightly bossed on dorsal surface.

Female unknown.

Origin. Description based on a single male collected by W. F. Cooper at Quamborne, New South Wales, Australia. Host, an iguana, species not stated.

Note. This species differs from *Aponomma ecinctum* in its possession of 3/3 rows of teeth on the hypostome and a pair of spurs on coxa I; from *Aponomma crassipes* in the absence of greenish iridescent spots on the bosses of the tarsi."

The main characters of the male *A. quadratum* appear to be: (i) the inornate scutum with 9 symmetrically arranged depressions on its posterior half, (ii) the indistinct marginal groove, (iii) the hypostome dentition of 3/3, (iv) the 2 spurs on coxa I, and (v) the slightly bossed, bicalcarate tarsi.

APONOMMA TRIMACULATUM (Lucas)

Plate 4, Figs. 1, 3; Fig. 8*a-h*

1878 *Ixodes trimaculatus* Lucas, p. 77.
1899 *Aponomma trimaculatum* (Lucas), Neumann, p. 187, fig. 41.
1900 *Aponomma trimaculatum* (Lucas), Froggatt, p. 3.
1913 *Aponomma trimaculatum* (Lucas), Patton and Cragg, p. 623.
1925 *Aponomma trimaculatum* (Lucas), Ferguson, p. 34.
1926 *Aponomma trimaculatum* (Lucas), Fielding, p. 92, fig. 36.
1928 *Aponomma trimaculatum* (Lucas), Sharif, p. 27.
1932 *Aponomma trimaculatum* (Lucas), Krijgsman and Ponto, p. 25.
1935 *Aponomma trimaculatum* (Lucas), Roberts, p. 6.
1944 *Aponomma trimaculatum* (Lucas), Toumanoff, p. 129.
1946 *Aponomma trimaculatum* (Lucas), Taylor, p. 124.
1947 *Aponomma gervaisi* (Lucas), Roberts, p. 11.

Larva unknown.

Nymph

Diagnosis

Scutum 0.68 by 0.93 mm., the postero-lateral margins slightly convex, punctations relatively large and distributed mainly laterally, hypostome dentition 3/3; coxae as in male; tarsi humped but without spurs.

Description

Body.—About as long as broad, 1.0 by 0.95 mm. (semi-engorged), scutum and capitulum brown, dorsum pale.

Scutum.—Much broader than long, 0.68 by 0.93 mm., posterior angle broad, postero-lateral margins slightly convex; punctations relatively large, few medianly and posteriorly, more numerous laterally, sometimes giving a somewhat rugose appearance to the lateral fields; cervical grooves continued posteriorly by very short, broad, and shallow, divergent depressions.

Capitulum.—Length 0.3 mm.; basis 0.25 mm., its dorsal anterior and lateral fields somewhat swollen, posterior margin slightly concave, the lateral margins rounded; hypostome dentition 3/3 of 7 or 8 teeth; palpi 0.2 mm. long, article 2 a little longer than article 3.

Spiracular plate.—Shape as in Figure 8*h*, 0.2 by 0.1 mm.

Legs.—Coxae with single spurs as in the male; tarsi humped and without spurs, tarsus I 0.30 mm. long, metatarsus 0.10 mm. long, tarsus IV 0.25 mm. long, metatarsus 0.15 mm. long.

Male

Diagnosis

A small tick measuring 1.50-1.90 by 1.60-1.90 mm., subcircular, ornate with 5 iridescent, green markings distributed as in *A. simplex*, but the lateral marking does not extend inwardly at its posterior extremity as it does in *A. simplex;* hypostome dentition, coxae, and tarsi as in *A. simplex.*

Description

Body.—Size 1.50-1.90 by 1.60-1.90 mm., subcircular and broadest towards the posterior third.

Scutum.—Ornate with 5 iridescent, greenish markings consisting of: (i) a small median mark, (ii) a pair of elongate lateral markings, and (iii) a pair of irregular, frequently semicircular, markings posteriorly on each side of the median longitudinal line and sometimes confluent with the lateral markings, otherwise brown; marginal groove absent; punctations numerous and distinct, most numerous laterally and posteriorly where many relatively coarse punctations are present, sometimes a number of coarse punctations also in the median field but punctations usually finer and more scattered here.

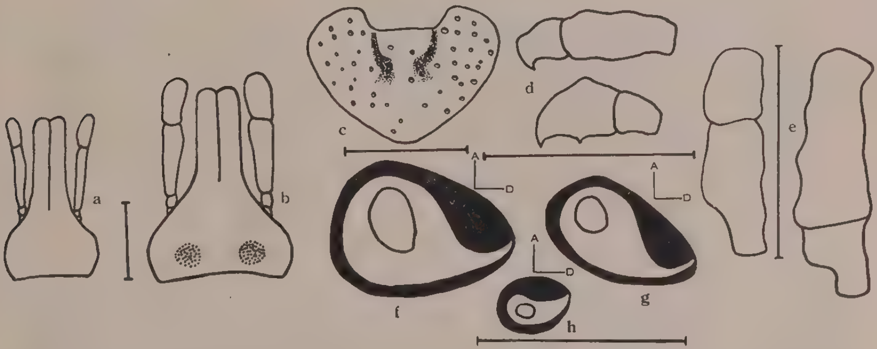

Fig. 8.—*Aponomma trimaculatum.* *a,* Capitulum of male (dorsal view); *b,* capitulum of female (dorsal view); *c,* scutum of nymph; *d,* tarsi I and IV of male; *e,* tarsi I and IV of female; *f,* spiracular plate of female; *g,* spiracular plate of male; *h,* spiracular plate of nymph. The straight lines each represent 0.5 mm.

Capitulum.—Length 0.66-0.76 mm.; basis 0.4-0.46 mm. wide, posterior margin almost straight, lateral margins slightly rounded; palpi 0.43-0.53 mm. long; hypostome dentition 4/4 of 8-10 teeth, the inner file of very small and delicate teeth.

Spiracular plate.—Shape as in Figure 8g, 0.4 by 0.2 mm.

Legs.—Coxae each with a single short, blunt spear; tarsi humped, tarsus I with a single terminal spur, other tarsi bicalcarate.

Female

Diagnosis

A small tick, scutum about as long as broad, ornate with 3 iridescent, green markings, the median one small; porose areas small, circular; hypostome dentition and coxae as in male; tarsi humped and without spurs.

Description

Body.—Size 2.5-4.0 by 1.9-2.7 mm.

Scutum.—Size 1.3-1.5 by 1.4-1.6 mm., about as broad as long, with broad, rounded lateral and posterior angles and slightly sinuous postero-lateral margins; ornate with 3 iridescent, green markings, 1 in each scapular field and a small one medianly; punctations numerous, uneven, but mainly relatively large, fairly evenly distributed, but sometimes least numerous in the posterior field; cervical grooves followed by broad, ill-defined, shallow, almost parallel depressions, which may extend almost to the scutal margin.

Capitulum.—Length 0.7-0.86 mm.; basis 0.53-0.6 mm. posterior border concave; porose areas small, circular, the interval greater than their diameter; palpi 0.5-0.56 mm. long; hypostome 4/4, teeth as in the male.

Spiracular plate—Shape as in Figure 8*f*, 0.4 by 0.26 mm.

Legs.—Relatively long; coxae as in the male; tarsi humped, without spurs.

Hosts and Distribution

A trimaculatum is recorded from India, Indo-China, the East Indies, and Australia. The writer has seen specimens also from New Guinea and the Solomon Is. In Australia, this species appears to be distributed mainly in the tropical areas, for the specimens in the material under examination were limited to north Queensland and the Northern Territory. The reptilian hosts included *Python amethystinus* (Schneider 1801), *Python* sp., and *Varanus* sp. There is also a record of the occurrence of this tick on a horse at Townsville.

Comments

A. trimaculatum is very closely allied to *A. simplex.* Both species have a similar hypostome dentition and similar ornamentation in both male and female. In the female *A. trimaculatum,* however, the median marking is much smaller than in the female *A. simplex,* and the inward extension of the posterior extremities of the lateral markings seen in the male of the latter species apparently does not occur in *A. trimaculatum.*

The male *A. trimaculatum* is smaller than the male *A. simplex* and, in the females, whereas the scutum of *A. simplex* is much broader than long, that of *A. trimaculatum* is about as long as broad. In the female scutum also, the number of punctations is much greater in *A. simplex.*

APONOMMA PULCHRUM, sp. nov.

Plate 4, Figs. 2, 4; Fig. 9*a-f*

Nymph and larva unknown.

Holotype.—Male from Rockhampton, Queensland, 8.iii.1906. Host, *Varanus* sp. In the Queensland Museum.

Allotype.—Female, same data. In the Queensland Museum.

Paratype.—One male, same data. In the collection of the Queensland Department of Agriculture and Stock, Animal Health Station, Yeerongpilly.

Male

Diagnosis

A small tick, subcircular, ornate with 9 iridescent, green markings; no marginal groove; hypostome dentition 3/3; coxae each with 1 spur; tarsus I with a terminal spur, other tarsi bicalcarate.

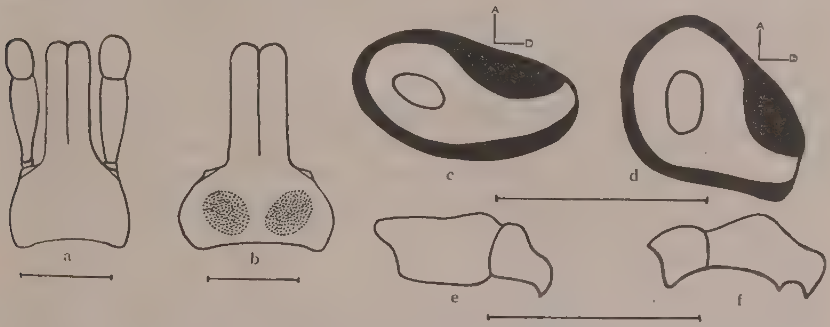

Fig. 9.—*Aponomma pulchrum.* *a,* Capitulum of male (dorsal view); *b,* capitulum of female (dorsal view); *c,* spiracular plate of male; *d,* spiracular plate of female; *e,* tarsus I of male; *f,* tarsus IV of male. The straight lines each represent 0.5 mm.

Description

Body.—Size 2.8 by 2.8 mm., subcircular and broadest posteriorly.

Scutum.—Brown, ornate with 9 iridescent, green markings consisting of (i) 1 in each scapular field, (ii) 1 elongate marking in each lateral field, (iii) 1 elongate marking internal to each lateral marking, (iv) a small posterior pair, and (v) a single median spot; marginal groove absent; punctations very numerous, fairly evenly distributed though somewhat denser and coarser laterally and posteriorly; cervical grooves short, deep, convergent; festoons distinct.

Capitulum.—Length 0.9 mm., brownish, darker at base of hypostome and on lateral margins; basis 0.56 mm. long, posterior margin slightly concave, lateral margins rounded, no obvious cornua; palpi 0.56 mm. long; hypostome dentition 3/3 of 7-9 teeth, the inner file teeth well developed.

Genital opening.—Opposite coxa II.

Spiracular plate.—Shape as in Figure 9*c*, dorsal prolongation pronounced, 0.53 by 0.32 mm.

Legs.—Coxae each with a single short, blunt spur, tarsus I 0.45 mm. long and 3 times as long as wide, metatarsus 0.30 mm. long, strongly humped and with a terminal spur, tarsi II-IV bicalcarate and strongly humped, tarsus IV 0.38 mm. long, metatarsus 0.12 mm. long.

Female

Diagnosis

A medium-sized species; scutum cordate with 3 iridescent, green markings; porose areas large, oval, divergent anteriorly; hypostome dentition 3/3; coxae as in male; all tarsi with a single terminal spur.

Description

Body.—A semi-engorged specimen, 7.3 by 5.5 mm., broadly oval and broadest in median third, dorsum very dark and furnished with scattered but evenly distributed, very short, pale hairs.

Scutum.—Size 1.7 by 2.0 mm., broader than long, heart-shaped, the posterior angle broad and rounded, the postero-lateral margins convex; dark brown in colour with 3 large, iridescent, green markings, 1 in each scapular field and 1 in the median field; punctations numerous, somewhat uneven, but well distributed, least numerous between the cervical grooves; cervical grooves short, deep, convergent, extended posteriorly by broad, shallow, parallel depressions, which do not attain the posterior margin.

Capitulum.—Length 0.83 mm.; basis 0.67 mm. wide, the posterior margin almost straight, the lateral borders rounded; porose areas, large, deep, oval, divergent anteriorly, the interval fairly narrow posteriorly; hypostome dentition as in the male; palpi missing.

Genital opening.—Opposite coxa II.

Spiracular plate.—Shape as in Figure 9*d*, 0.6 by 0.36 mm.

Legs.—Coxal spurs as in male; tarsi similar to those of the male, but with a single small, terminal spur only.

Comments

This species shows a very close resemblance to the African species *A. exornatum* Koch, but differs mainly in the shape and punctations of the female scutum and in the number of spurs on coxa I, there being 2 of these spurs in *A. exornatum*. It may be readily separated from *A. simplex* and *A. trimaculatum* by the hypostone dentition, which has the formula 3/3.

Genus AMBLYOMMA C. L. Koch

1844 *Amblyomma* C. L. Koch, p. 223.

The genus *Amblyomma* possesses the following characters; scutum generally ornate with dark stripes and spots on a pale ground; capitulum long; eyes and festoons present; anal groove encircling the anus behind; male without adanal plates, but ventral plaques may be present; spiracular plates subtriangular or comma-shaped.

Seven species of this genus have been recorded from Australia, namely *A. triguttatum* Koch 1844, *A. helvolum* Koch 1844, *A. moreliae* (L. Koch 1867), *A. limbatum* Neumann 1899, *A. postoculatum* Neumann 1899, *A. australiense* Neumann 1905, and *A. albolimbatum* Neumann 1907. In the material at the disposal of the writer, all these species were recognized except *A. helvolum* and *A. postoculatum*. *A. papuana* Hirst 1914, previously known only from Dutch New Guinea, is recorded from Australia for the first time. Four new species were seen.

Species of *Amblyomma* are highly important parasites of domestic animals and man in Africa and America. *A. hebraeum* Koch 1844 is a vector of heartwater of sheep, cattle, and goats and of tick-bite fever of man in central and South Africa. *A. variegatum* (Fabr. 1794) transmits heartwater in Kenya and also Nairobe sheep disease. The important American species include *A. americanum* (Linn. 1758), a vector of human tick typhus, tularaemia, and Q fever, and *A. maculatum* Koch 1844, a serious parasite of livestock in the Gulf Coast areas of the United States, whose bite is very attractive to the screw-worm fly, *Calletroga americana* Cushing & Patton 1933. *A. cayennense* (Fabr. 1787) transmits the Brazilian strain of human tick typhus and is a serious pest of cattle in tropical America, infestations being a source of attraction to the tropical warble fly, *Dermatobia hominis* (Linn. 1758).

The Australian species are normally parasites of native fauna, and many species of Reptilia, the kangaroo, and other marsupials, the dingo, and the spiny ant-eater are included among their hosts. Two species have been recorded from livestock, namely *A. moreliae* and *A. triguttatum*. The former has been found on the ox and the horse and is one of the commonest and most widespread reptilian ticks in eastern Australia. Its occurrence on these domestic animals is regarded as fortuitous and of no importance. *A. triguttatum* is a common parasite of the ox, horse, and sheep in northern Australia. Infestations usually do not consist of more than a few ticks and the economic importance of this species is restricted mainly to the confusion that may arise when it is mistaken by the layman for the cattle tick, *Boophilus microplus* (Canes. 1887). Its role as a vector of the cattle tick-fever organisms has not been explored.

All the Australian species are ornate, except *A. australiense*. There is frequently some variation in the colour pattern of the ornate species and, as furthermore, the colour may fade after preservation in alcohol, the ornamentation pattern is not regarded as a good specific character. Three species, namely *A. helvolum*, *A. postoculatum*, and *A. sternae*, have a hypostome dentition formula of 3/3; in the others it is 4/4. *A. papuana* is the only species with 2 spurs on coxae II-IV; in the others there is only 1 spur on each of these coxae. The males of the Australian *Amblyomma* spp. can be readily distinguished, but it has been difficult to find outstanding characters for some of the females, particularly those of *A. moreliae*, *A. limbatum*, and *A. albolimbatum*.

KEY TO AUSTRALIAN SPECIES OF THE GENUS AMBLYOMMA

*Males**

1. Marginal groove complete and well defined 2
Marginal groove incomplete, ill defined, or absent 3

2 (1). Marginal groove wide and shallow posteriorly with numerous fine longitudinal ridges; hypostome dentition formula 4/4 .... *A. triguttatum*
Marginal groove narrow and of even width, without fine longitudinal ridges; hypostome dentition formula 3/3 .... *A. sternae*

3 (1). Coxae II-IV each with 2 widely separated spurs .... *A. papuana*
Coxae II-IV each with a single spur 4

4 (3). Basis capituli with strong cornua; scapular angles each with a small, anteriorly directed spine .... *A. macropi*
Basis capituli devoid of strong cornua; scapular angles without such a spine 5

5 (4). Inornate; marginal groove interrupted behind the eye; scapular angles ventri-flexed .... *A. australiense*
Ornate; marginal groove, if present, not interrupted behind the eye; scapular angles not ventri-flexed 6

6 (5). Hypostome dentition formula 3/3; marginal groove absent; scutum with 6 symmetrically placed, pale, marginal spots and 1 anterior median spot .... *A. helvolum*
Hypostome dentition formula 4/4; marginal groove present but may be ill defined; scutal ornamentation not as above 7

7 (6). Coxa IV with a long, acute spur, much longer than the spurs on coxae II and III .... *A. albolimbatum*
Coxa IV with a medium or short spur at most only slightly longer than the spurs on coxae II and III 8

8 (7). Marginal groove distinct and deep, extending from the external festoon to near the eyes .... *A. moreliae*
Marginal groove ill defined, apparent for only a short distance extending from the external festoon .... *A. limbatum*

Females†

1. Coxae II-IV each with 2 widely separated spurs .... *A. papuana*
Coxae II-IV each with a single spur 2

2 (1). Coxa IV with a long, acute spur, much longer than the spurs on coxae II and III .... *A. moyi*
Coxa IV with a medium or short spur, at most only a little longer than the spurs on coxae II and III 3

3 (2). Hypostome dentition formula 3/3 4
Hypostome dentition formula 4/4 6

4 (3). Large tick, the scutum very rugose, article 2 of palpi about 2½ times as long as article 3 .... *A. sternae*
Small tick, the scutum not rugose, article 2 of palpi at most twice as long as article 3 5

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* The males of *A. postoculatum, A. moyi,* and *A. echidnae* are unknown.

† The female of *A. macropi* is unknown.

5 (4). Scutum triangular, dorsum thickly beset with large, flat, pale hairs *A. postoculatum*
Scutum cordiform, dorsum without such hairs.................... *A. helvolum*

6 (3). Scutum inornate, punctations few and fine...................... *A. australiense*
Scutum ornate, several coarse punctations present, particularly in the lateral fields..7

7 (6). Basis capituli with a depression, usually double, in the interval and a deep, curved groove between each porose area and the lateral margin........ *A. triguttatum*
Basis capituli without such depressions and grooves.........................8

8 (7). Porose areas relatively small, the interval about 1½ times to twice their diameter; scutal punctations relatively few and mainly fine................ *A. limbatum*
Porose areas moderate to large, the interval equal at most to their diameter; scutum with many coarse punctations......................................9

9 (8). Posterior margin of basis capituli markedly concave................ *A. echidnae*
Posterior margin of basis capituli straight or at most only slightly concave........10

10 (9). Coarse punctations in scapular and lateral fields fairly well distributed; no depression in scutum near eye.............................. *A. albolimbatum*
Coarse punctations practically confined to the mid-lateral field, usually with some confluency to form a conspicuous depression near eye.............. *A. moreliae*

Notes on Known Species

AMBLYOMMA PAPUANA Hirst

1914 Hirst, p. 327, fig. 15.

This species was represented by 4 males and 2 females taken from a "spiny ant-eater" at Cairns, north Queensland.

The male is a small subcircular, *Aponomma*-like tick with an indistinct colour pattern that includes 2 extensive patches near the posterior margin and traces of colour in the adjoining lateral areas. Scutal punctations are numerous and mainly coarse, particularly laterally and posteriorly. The festoons are poorly developed and hardly visible dorsally. The basis capituli has salient and raised postero-lateral angles and the hypostome dentition is 4/4. All coxae have 2 widely separated spurs and trochanters II-IV have each a single spur.

The female is a relatively small tick even when fully engorged. The scutum has numerous coarse punctations and a pale spot in each scapular field reaching to the antero-lateral border. The lateral angles of the basis capituli are raised and somewhat salient and the porose areas encroach on the posterior margin. The hypostome dentition and coxal and trochantal spurs are similar to those of the male.

AMBLYOMMA POSTOCULATUM Neumann

1899 Neumann, p. 232.

This species was described by Neumann from a single female from an unknown host from King I.

According to the descriptions given by Neumann (1899) and by Robinson (1926), *A. postoculatum* may be distinguished by the dense, long, flattened, whitish hairs that cover the dorsum, by the extensive ornamentation of the scutum, by the somewhat large and closely approximated areas, and by the hypostome dentition of 3/3.

AMBLYOMMA HELVOLUM Koch

1844 Koch, p. 230.

This small, *Aponomma*-like species is recorded from the Nicobar Is. (India), Indo-China, Malaya, East Indies, Philippine Is., and Australia. Robinson (1926) is responsible for the Australian record and refers to a single female taken from *Varanus* sp. by W. F. Cooper at Quambone, N.S.W. It has not been seen by the writer among the material available for examination.

Detailed descriptions of the male and female are given by Robinson (1926). It superficially resembles *Aponomma simplex* recorded from *Varanus* sp., Quambone, by Cooper and Robinson (1908) and from which it differs mainly by the hypostome dentition of 3/3 and by the possession of eyes.

AMBLYOMMA AUSTRALIENSE Neumann

1905 Neumann, p. 227.

This species was described by Neumann from the spiny ant-eater, *Tachyglossus aculeatus* Shaw & Nodder 1792, in Western Australia. Robinson records it from the "iguana" at Darwin, Northern Territory. The writer has never encountered it in Queensland, but there is a record by Taylor (1911) of its occurrence on *T. aculeatus* at Townsville. Taylor's notes, however, do not mention any of the more salient distinguishing features of this species.

A. australiense is an inornate species with the scapular angles terminating in deflected, conical points. The male has an incomplete but well-defined marginal groove terminating at the external festoon and interrupted behind the eye. The punctations of the scutum are fine and distributed mainly posteriorly and laterally. The posterior margin of the basis capituli is, in both sexes, concave with salient postero-lateral angles. The female scutum has a very broad posterior angle and a deep depression in each laterial field near the eye. Punctations are few and fine.

AMBLYOMMA MORELIAE (L. Koch)

1867 L. Koch, p. 241.

This is a common and widespread tick on Reptilia in Queensland, its hosts including many species of snakes and lizards. It has also been taken in this State from the horse, ox, and man. It is a common species on Reptilia also in New South Wales (Ferguson 1925), and has been seen by the writer from several species of snakes in Victoria. Taylor (1911) records it from the Northern Territory. Fielding (1911) places *Macropus* sp. among its hosts.

The males of *A. moreliae* may be readily recognized by the incomplete but well-defined marginal groove, which extends from near the eyes to the external festoons, by the colour pattern, by the relatively few punctations, most of which occur in the scapular fields and in the marginal areas, and by the short spurs on the coxae. Robinson (1926) describes the ornamentation as comprising an irregular, pale spot in each scapular angle and 2 or 3 smaller spots on the marginal ridge. In the specimens seen by the writer, these pale areas are frequently connected by a thin bridge along the inner edge of the marginal groove, sometimes extending posteriorly to reach the first and second and occasionally the third festoon. In other specimens, the connecting bridge is missing, but the posterior spots are visible.

The female colour pattern also varies. Many specimens have the colour confined to a single irregular, pale spot in each scapular field as figured by Robinson (1926); in others there is also a small, pale spot in the posterior angle. In other females again, the coloration is much more extensive and the scapular spot may be extended towards the cervical groove as in *A. limbatum*, this extension being sometimes isolated. In a few specimens the scapular spot has extended posteriorly as well so that distinct cervical spots and stripes, ocular spots, and limiting spots are visible.

The posterior margin of the basis capituli is usually straight, at most only slightly concave. The porose areas are large and circular with the interval about equal to their diameter. The scutum is usually cordiform, but sometimes the postero-lateral margins are straight and the scutum approaches a triangular appearance. The coarse punctations of the scutum are relatively few and grouped together in the mid-lateral field and in most specimens there is a short, narrow depression on their outer margin near the eye.

AMBLYOMMA ALBOLIMBATUM Neumann

1907 Neumann, p. 218.

This tick was described by Neumann from *Trachysaurus rugosus* Gray 1827 in Western Australia where it is a common parasite of this lizard. Johnstone (1932) records it from the same host in South Australia and Ferguson (1925) in New South Wales. The writer has seen specimens from *T. rugosus* from Victoria. Robinson (1926) includes *Diemenia superciliosa* (Spin. 1894) as another Western Australian host, and Ferguson (1925) has found this tick on *Notechis scutatus* Kinghorn 1921 in New South Wales.

It has not been seen by the writer among Queensland material, but Fielding (1911) records it from *Varanus varius* (Shaw 1790) in north Queensland.

The male may be readily distinguished by its ornamentation, the punctation pattern, the appearance of the cervical grooves, the short and poorly developed marginal groove, and by the long spur on coxa IV.

In the female, the scutum has a very broad posterior angle and convex postero-lateral margins. The punctations in the lateral fields are well distributed and numerous, more so than in *A. moreliae, A. limbatum,* and *A. echidnae,* and include many relatively coarse punctations. *A. albolimbatum* also differs from these species in the absence of a depression in the scutum near the eye. The ornamentation follows the description given by Robinson (1926), but occasionally a small additional pale patch may be present in the posterior angle.

AMBLYOMMA LIMBATUM Neumann

1899 Neumann, p. 231.

A. limbatum was described by Neumann from unspecified hosts from King I., Tasmania, and Adelaide, S.A.

Specimens from snake hosts have been seen by the writer from Victoria and also from Queensland. It appears to be a rare tick in Queensland. Robinson (1926) records it from a carpet snake, Northern Territory. There is a female from *Varanus* sp. in the collection of the Animal Health Station, Yeerongpilly, also from this part of Australia.

The males examined agreed closely with Robinson's description. In some specimens the lateral coloration is separated into isolated patches and in others these patches are joined by thin bridges. The male may be readily recognized by its small size, by its scutal colour and punctation pattern, by the poorly developed, almost obsolete, marginal groove, and by the coxal armature.

The coloration of the female scutum is usually of the pattern described and figured by Robinson (1926). Two females have been seen with a more extensive pattern. In these, the scapular patch is forked and continued posteriorly and the patch in the posterior angle is greatly increased in size and continued anteriorly towards each cervical depression. In a few specimens there is a short row of confluent punctations laterally near each eye. Usually, however, punctations are few and fine and in the lateral fields coarse punctations are rarely seen. The scutal punctation pattern, the relatively small porose areas placed at an interval of 1½ times to twice their diameter, and the coxal armature are the main distinguishing features of the females.

AMBLYOMMA TRIGUTTATUM Koch

1844 Koch, p. 225.

An extensive series of this species was available for examination.

The typical male is described and figured by Robinson (1926) as possessing a pale patch in each lateral field extending anteriorly in some specimens into the scapular field and terminating posteriorly a little in front of the external festoon. There are also a pair of pale spots posteriorly and medianly on each side of the fifth festoon.

Robinson also refers to males in which the ornamentation is more extensive. In these the postero-median and antero-accessory stripes stand out clearly, the postero-accessory stripes are represented by dark patches flattened alongside the marginal groove, and the 3 lateral spots are confused in a dark, elongate stripe running along the internal border of the marginal groove. The outline of a pseudo-scutum is clearly seen.

In the series examined by the writer there were a number of males in which the ornamentation varied between these two descriptions and in some of which small ornate patches were present also on the festoons. In the more ornate males the coarse punctations of the scutum are usually less numerous in the antero-median and median fields.

Other characters appear to be more constant. The marginal groove is continuous, narrow, and deep anteriorly, wide and shallow posteriorly, with numerous fine longitudinal ridges extending to the inner border of the marginal ridge.

In the females the ornamentation and punctations of the scutum are also variable. The typical female has a pale spot in the posterior angle and sometimes a pale spot in the antero-lateral field. The punctations are very numerous and uneven, mainly coarse in the lateral and scapular fields and sometimes also in the posterior angle so that these areas appear rugose. In other females, the ornamentation is more extensive and includes a large part of the lateral field, extending almost to the postero-lateral margin. The spot in the posterior angle is much larger and sometimes extends into the median field. In the more ornate females, the punctations are less numerous, the coarser punctations being mainly in the lateral fields.

The scutum also shows considerable variation in its dimensions and in the less ornate females the scutum is larger, almost twice as large in many specimens as that of the more ornate specimens.

The double, central depression between the porose areas and the curved depressions between these structures and the lateral border of the basis capituli are usually fairly well defined. They are always present, though more developed in some females than in others.

It is possible that *A. triguttatum* as at present defined may be a complex of more than one species. Highly ornate males, however, and the less ornate females may occur together on the same host and vice versa. The more ornate specimens formed a minority in the collections examined and were taken from Queensland and the Northern Territory.

A. triguttatum is widespread throughout Queensland and the Northern Territory. Its distribution extends into New South Wales, South Australia, and Western Australia. It appears to be distributed mainly in the northern half of the Commonwealth.

This is a common tick on the kangaroo, wallaroo, and wallaby. It has also been taken from the dingo, platypus, cattle, horse, sheep, dog, and man. It is a very common species on cattle, engorged females measuring up to nearly 22 mm. on this host.

The larva and nymph of *A. triguttatum* have not been previously described. The descriptions given below were taken from larvae bred by Mr. P. J. O'Sullivan, Parasitologist, Animal Health Station, Yeerongpilly, from eggs laid by a typical female. The nymphs were obtained by feeding these larvae on rabbits and cattle.

Larva

Fig. 10*c,d,h,i*

Diagnosis

Scutum 0.30-0.33 by 0.43-0.45 mm., antero-lateral margins long, postero-lateral margins concave, finely rugose; cervical grooves leading into short, somewhat parallel depressions; hypostome dentition 2/2; coxa I with 2 spurs, the external spur longer than the internal spur, coxae II-IV each with a single spur.

Description

Body.—Unengorged, length 0.64 mm., breadth 0.53 mm., pale with slightly darker capitulum, scutum, and legs; oval, broadest medianly, with conspicuous festoons; fully engorged, length 1.0 mm., breadth 0.75 mm.; legs, scutum, and capitulum dark brown, dorsum with scattered, very small, pale hairs.

Scutum.—Length 0.30-0.33 mm., 0.43-0.45 mm. wide, broader than long, posterior angle broad, antero-lateral margins long, postero-lateral margins concave; finely rugose but with no apparent punctations; cervical grooves very short, somewhat convergent, followed by short, almost parallel depressions, which extend about half the length of the scutum; eyes large and pale.

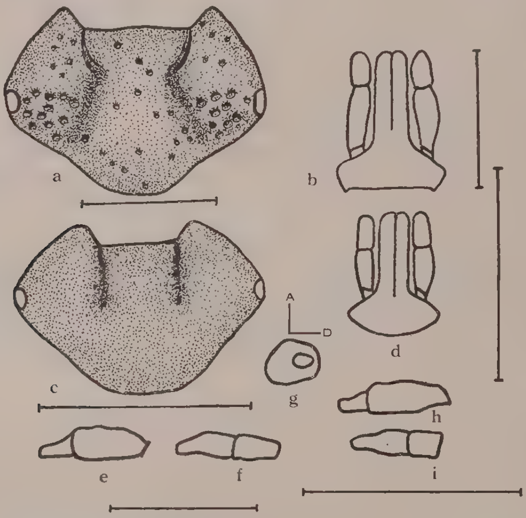

Fig. 10.—*Amblyomma triguttatum*. *a,* Scutum of nymph; *b,* capitulum of nymph (dorsal view); *c,* scutum of larva; *d,* capitulum of larva (dorsal view); *e,* tarsus I of nymph; *f,* tarsus IV of nymph; *g,* spiracular plate of nymph; *h,* tarsus I of larva; *i,* tarsus IV of larva. The straight lines each represent 0.5 mm.

Capitulum.—Length 0.21 mm.; basis triangular, 0.18 mm. wide, posterior margin convex; palpi 0.14 mm. long, article 2 a little longer than article 3; hypostome 2/2 of 4-6 teeth.

Venter.—Pale with few scattered, small, pale hairs.

Legs.—Coxa I with 2 small spurs, the external spur longer than the internal spur, coxae II and III each with a single small spur; tarsus I 0.23 mm. long, metatarsus 0.16 mm. long, tarsi II and III a little smaller than tarsus I, metatarsi about 0.07 mm. long.

Nymph

Fig. 10*a,b,e,f,g*

Diagnosis

Scutum 0.82 by 1.0 mm., some large, coarse punctations in the lateral fields, postero-lateral margins usually straight; basis capituli trapezoidal in shape, the postero-lateral angles sharp; hypostome dentition 3/3, the inner file frequently small; coxae as in larva.

Description

Body.—Unfed, length 1.8 mm., breadth 1.34 mm.; fully engorged, length 2.8 mm., breadth 2.2 mm.; dorsum with numerous evenly distributed, relatively long, pale hairs, festoons conspicuous in unfed specimens but inapparent in engorged nymphs.

Scutum.—Length 0.82 mm., 1.0 mm. wide; brown, sometimes darker near eyes, broader than long, finely rugose with some large, coarse punctations in lateral fields and a few fine punctations elsewhere; posterior angle broad, postero-lateral margins straight, sometimes a little sinuous; eyes conspicuous, large; cervical grooves short, deep, convergent, continued posteriorly by diverging depressions, which become shallow and broad, but do not quite attain the postero-lateral margins.

Capitulum.—Length 0.47 mm.; basis 0.40 mm. wide, pale brown, darker at postero-lateral angles; posterior margin concave, lateral margins straight and divergent to give basis a trapezoidal shape; postero-lateral angles sharp and raised but not conspicuously so, slightly salient; palpi 0.4 mm. long, article 2 about twice as long as article 3; hypostome 3/3 of 5 or 6 teeth, the inner file frequently small.

Venter.—Practically without any hairs except posteriorly.

Legs.—Pale brown; coxa I with 2 conspicuous spurs, the outer longer than the inner, coxae II-IV each with a single very small spur; tarsus I 0.44 mm. long, the metatarsus 0.3 mm. long, other tarsi smaller, about 0.37 mm. long, their metatarsi 0.14 mm. long.

Spiracular plate.—Shape as in Figure 10*g*, 0.2 by 0.18 mm.

Nymphs agreeing with the above description have been taken from cattle and kangaroos in Queensland.

Description of New Species

AMBLYOMMA MOYI, sp. nov.

Fig. 11*a-f*

Holotype.—Female found in kangaroo cave, Mt. Isa, Queensland, October 1940 (G. Moy). In the Queensland Museum.

Paratype.—Female, same data, in the Queensland Museum.

Diagnosis

A medium-sized tick; scutum slightly broader than long, ornate with a pale patch in each lateral field and a pair of short but deep depressions near the eyes; porose areas large, oval, divergent; hypostome dentition 4/4; coxa I with 2 spurs, the external spur long and acute, coxae II and III each with a single short spur, coxa IV with a long, acute spur; tarsus I with a single slight spur, other tarsi bicalcarate.

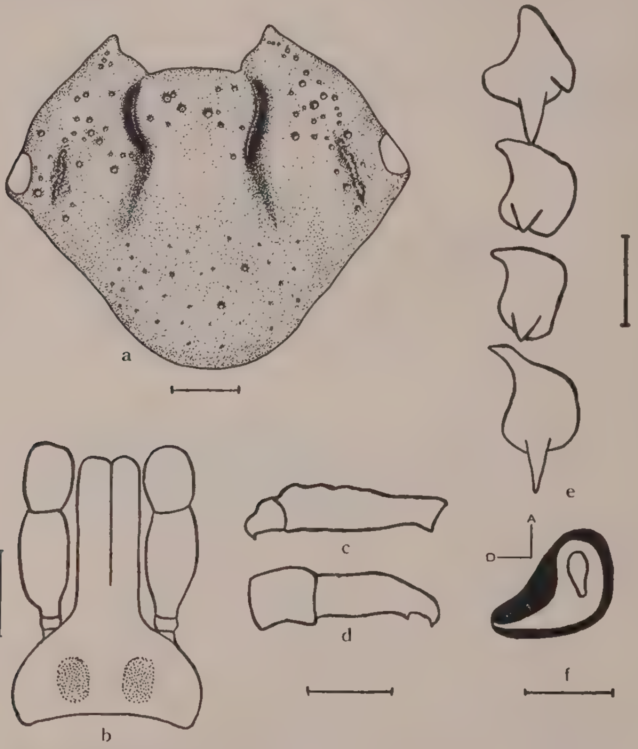

Fig. 11.—*Amblyomma moyi* (female). *a*, scutum; *b*, capitulum (dorsal view); *c*, tarsus I; *d*, tarsus IV; *e*, coxae I-IV; *f*, spiracular plate. The straight lines each represent 0.5 mm.

Description

Body.—Unfed, length 6.6 mm., breadth 4.1 mm., flat, oval, widest in region of spiracles; scutum grey-brown, ornate; dorsum with small, scattered, pale hairs; dorsal grooves well defined; festoons conspicuous.

Scutum.—Length 2.6 mm., 2.8 mm. wide; slightly broader than long; posterior angle moderately broad and rounded, postero-lateral margins slightly sinuous; eyes large and flat; a pale patch in each scapular field, otherwise brown; punctations not numerous, uneven, few and mainly fine in posterior and median fields, several moderately coarse but shallow punctations in lateral fields mainly anterior to a pair of short but deep depressions near the level of the eyes, a few small to moderate punctations in the scapular fields; cervical grooves short, deep, and convergent, continued posteriorly by somewhat divergent, deep depressions, which become shallow and extend into the posterior half of the scutum.

Capitulum.—Length 1.6 mm.; basis 1.1 mm. wide, the posterior margin concave, the postero-lateral angles rounded, raised, and slightly salient; porose areas large, oval, their long axes slightly divergent anteriorly, the interval wider than their diameter; palpi stout, 1.2 mm. long, article 2 less than 1½ times article 3; hypostome dentition 4/4 of 6 or 7 teeth.

Venter.—Dark, with some scattered, small hairs and well-marked grooves; genital opening between coxae II and III.

Legs.—Brown, strong, and of moderate length; coxa I with 2 unequal spurs, the external long and acute and much longer than the internal, coxae II and III each with a single small spur, coxa IV with a single long spur about equal in size to the external spur on coxa I; tarsus I with a single inconspicuous, terminal spur, metatarsus almost 4/5 of tarsus, tarsi II-IV more slender, attenuating to tallus less abruptly than tarsus I, bicalcarate.

Spiracular plate.—For shape see Figure 11*f;* 0.7 by 0.6 mm.

Comments

In the paratype, the porose areas are almost subcircular, with a narrower interval. The coloration is more extensive, occupying a greater area in the lateral fields extending to the cervical groove and continuing posteriorly as 2 branches on either side of the depression near the eyes, the outer branch being very narrow. Both specimens were preserved in alcohol and the pale areas are poorly defined.

AMBLYOMMA MACROPI, sp. nov.

Fig. 12*a*-*g*

Holotype.—Male, Ingham, north Queensland, 8.x.1917. Host, kangaroo. In the Queensland Museum.

Diagnosis

A medium-sized tick, scutum ornate with a pale patch in each scapular field and on each side external to marginal groove; marginal groove distinct, incomplete, represented posteriorly by coarse punctations; scapular points with a small but distinct spine; cornua well developed; hypostome dentition 4/4; coxa I with 2 spurs, the external long and acute, coxae II and III each with a single short spur, coxa IV with a long, acute spur.

Description

Body.—Length 5.0 mm., width 3.5 mm.; flat, oval, dark brown with pale markings.

Scutum.—Punctations moderately numerous, uneven, the coarser punctations distributed mainly laterally and posteriorly, a group of fine punctations near the external festoon and visible on one side only; a pale patch in each scapular angle and 2 small, isolated patches on each side external to the marginal groove; marginal groove distinct, deep but incomplete, commencing a little above the level of the eyes and continuing to the anterior border of the external festoon, and represented posteriorly by coarse punctations, some of which are confluent; scapular points with a small but conspicuous spine-like process directed anteriorly; eyes flat, not prominent; cervical grooves short, deep, convergent; festoons separated by deep grooves, the second festoon being larger than the others.

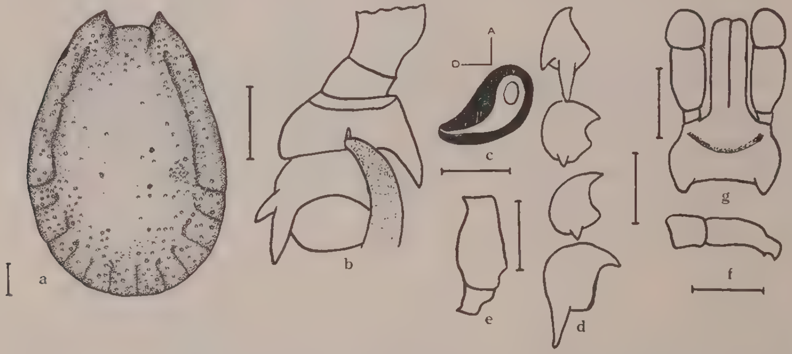

Fig. 12.—*Amblyomma macropi* (male). *a,* Scutum; *b,* lateral view of scapular points and basis capituli; *c,* spiracular plate; *d,* coxae I-IV; *e,* tarsus I; *f,* tarsus IV; *g,* capitulum of male (dorsal view). The straight lines each represent 0.5 mm.

Capitulum.—Length 1.5 mm.; basis 0.80 mm. wide, the posterior border concave with well-developed cornua, the lateral margins convex; palpi stout, 0.8 mm. long, article 2 a little less than twice the length of article 3; hypostome dentition formula 4/4 of 7-9 rather crowded teeth, small posteriorly, denticles poorly developed and in 9 or 10 rows.

Venter.—Dark, wrinkled, with small, pale hairs and many scattered, fine punctations; genital opening prominent, between coxae II; genital and anal grooves well developed, the latter broadly U-shaped.

Legs.—Brown with pale joints; coxa I with 2 unequal spurs, the external spur long and acute, much longer and stouter than the internal spur, coxae II and III each with a single short spur about equal in size to the internal spur on coxa I, coxa IV with a single long, acute spur; tarsus I broad and slightly humped, attenuating rather abruptly and with a small, terminal spur, metatarsus about four-fifths the length of tarsus, tarsi II-IV not as stout as tarsus I and attenuating more gradually, bicalcarate, the terminal spurs well developed, the inner spurs comparatively weak.

Spiracular plate.—Shape as in Figure 12*c*, 0.5 mm. long.

Comments

The ornamentation of this specimen has faded badly. The pale patches mentioned in the description can be seen distinctly, but there are indications that the ornamentation may also involve a pair of rather large patches laterally, another pair posteriorly and medianly, and a small patch on each festoon.

AMBLYOMMA STERNAE, sp. nov.

Holotype.—Male, Green I. (near Cairns), north Queensland, August 1914. Host, sooty tern (*Sterna fuscata* Linn. 1758). In the Queensland Museum.

Allotype.—Female; same data as holotype. In the Queensland Museum.

Paratype.—Female, same data as holotype. In the collection of the Animal Health Station, Yeerongpilly, Queensland.

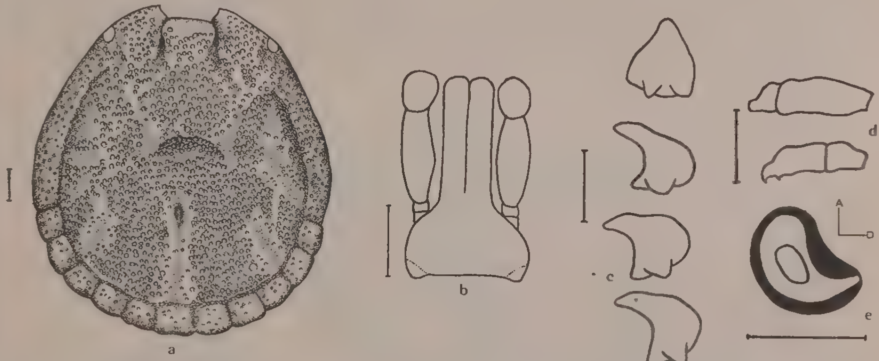

Fig. 13.—*Amblyomma sternae* (male). *a*, Scutum; *b*, capitulum (dorsal view); *c*, coxae I-IV; *d*, tarsi I and IV; *e*, spiracular plate. The straight lines each represent 0.5 mm.

Male

Fig. 13*a-e*

Diagnosis

A large, subcircular tick with brownish stripes and spots on an extensive metallic, golden background; punctations numerous and mainly coarse, a crescentic depression of confluent punctations medianly; marginal groove complete; hypostome dentition 3/3; coxa I with 2 subequal, short spurs, other coxae each with a single spur.

Description

Body.—Length 5.4 mm., width 4.8 mm., broadly oval and convex with some scattered, small, pale hairs.

Scutum.—Extensively ornate with brownish stripes and spots on a metallic golden ground (alcohol preservation); postero-median stripe narrow, interrupted medianly and somewhat swollen anteriorly, not reaching the falciform stripe; postero-accessory stripes narrow, of medium length, and directed towards the centre of the scutum, a large brownish spot with splashes of colour posteriorly between the postero-accessory and the postero-median stripes, which reach the falciform stripe; lateral spots irregular, on one side all attaining the marginal groove, on the other side the second spot isolated; frontal spot small and indefinite; falciform stripe broad, its lateral extremities fused with the broad antero-accessory stripes, which may reach the frontal spot; cervical spot dark, fused with the dark, divergent cervical stripes; a medium-sized brown area between the anterior accessory stripes; a dark border commencing at the ocular spot and extending along the lateral and posterior margins with 4 indentations on each side between the eyes and external festoons; festoons well defined and broader than long, each with a coloured patch; punctations very numerous, close together, mainly coarse, with some confluency to give scutum a rugose appearance, relatively few in the region of the postero-median and postero-accessory stripes and of the lateral spots, a crescentic depression of confluent punctations in the median field; marginal groove complete, of even width, commencing a little behind the eyes; cervical grooves short, deep, and convergent.

Capitulum.—Length 1.4 mm.; basis 0.88 mm. wide with an ornate patch and some rugosity dorsally, posterior margin concave, the postero-lateral corners rounded and somewhat prominent, lateral margins convex, palpi 0.88 mm. long, article 2 more than twice the length of article 3; hypostome dentition formula 3/3 with 5-7 teeth.

Venter.—Pale brown with several rows of very small, pale hairs; genital opening between coxae II; ventral grooves well defined.

Legs.—Brown and well developed; coxa I with 2 short, broad, blunt, subequal spurs, coxae II-IV each with a single short spur, tarsus I stout, attenuating rather abruptly, no obvious spurs, tarsi II-IV each bicalcarate.

Spiracular plate.—Shape as in Figure 13*e*.

Female

Fig. 14*a-c*

Diagnosis

A large tick; scutum cordiform, highly ornate, punctations mainly coarse, numerous, confluent and extending to postero-lateral margins; cervical grooves deep, leading into broad, deep, divergent depressions; porose areas large, irregular, and broadly oval, divergent anteriorly; hypostome dentition as in the male.

Description

Body.—Engorged; length 20.0 mm., breadth 15.2 mm., broadly oval; dorsum with numerous long, pale hairs; dorsal grooves visible, festoons not obvious.

Scutum.—Length 3.1 mm., breadth 3.5 mm., cordiform, the posterior angle not particularly broad, emargination deep, scapular points somewhat deflected;

cervical grooves deep, convergent, continued posteriorly by broad, deep depressions, which diverge slightly, become shallow, and extend a short distance into the posterior half of the scutum; punctations very numerous, uneven, mainly coarse, deep, confluent in places, well distributed, and extending to the margin; ornamentation extensive, metallic golden on a brown background (alcohol preservation); a dark narrow margin, broadest along the anterior borders and including the emargination, absent from the posterior angle; cervical spots dark, fused with the cervical stripes, which are swollen near the cervical groove and are connected with the limiting spots by a narrow bridge; limiting spots small and narrow, frontal spot small, narrowly attaining the margin, ocular spot dark and small; eyes large and flat.

Capitulum.—Length 1.8 mm.; basis 1.2 mm. wide, posterior margin concave with rounded, swollen, and slightly salient postero-lateral angles, lateral margins convex, porose areas, large, irregularly and broadly oval, their long axis lying anteriorly and posteriorly and slightly divergent anteriorly, the interval depressed and less than their transverse diameter; palpi 1.2 mm. long, stout, article 2 about 2½ times article 3; hypostome dentition formula 3/3 of about 6 rather small teeth.

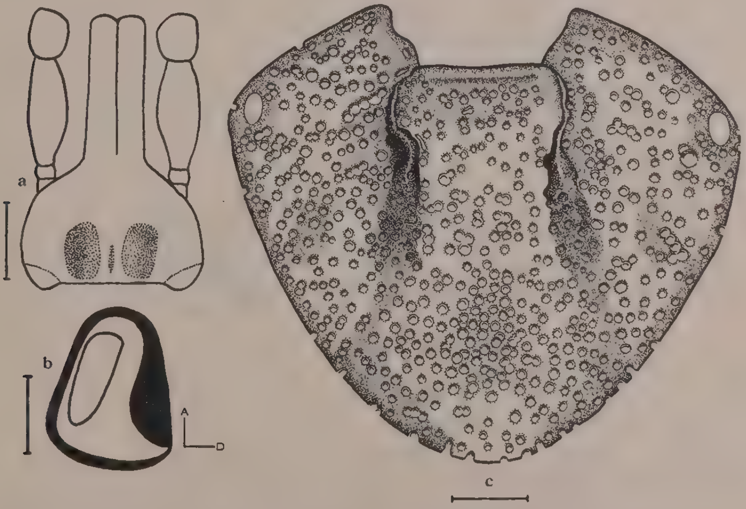

Fig. 14.—*Amblyomma sternae* (female).—*a*, Capitulum (dorsal view); *b*, spiracular plate; *c*, scutum. The straight lines each represent 0.5 mm.

Venter.—Dark with scattered, pale hairs, grooves well developed, genital opening anterior to coxa II.

Legs.—Well developed, coxae as in the male but the spurs are generally shorter and broader, those on coxae II and III particularly so; tarsi attenuating more gently than in the male.

Spiracular plate.—Shape as in Figure 14*b*.

Comments

The paratype is larger than the allotype and agrees in all particulars except that the cervical stripe is narrowly separated from the limiting spot. Its scutum measures 3.2 by 3.6 mm.

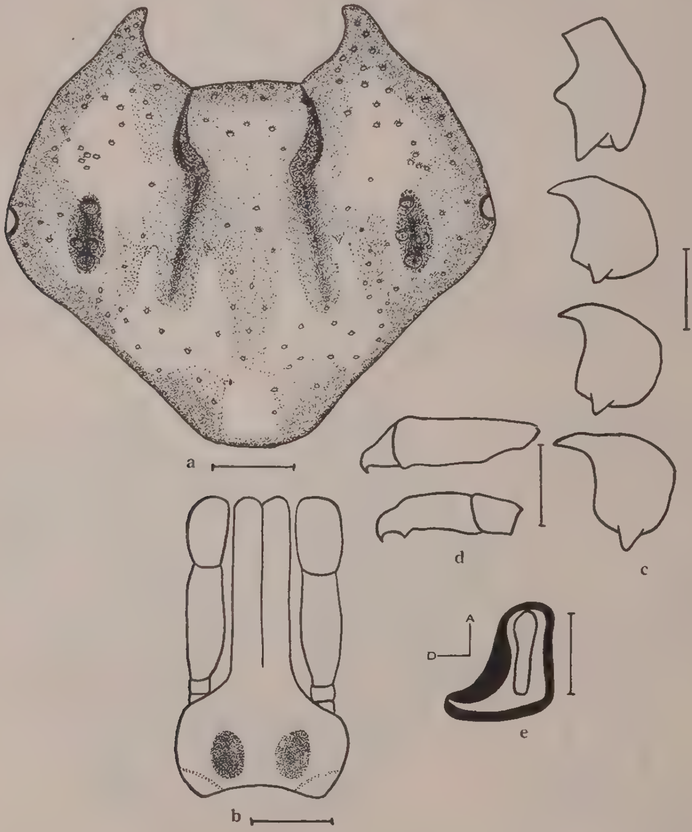

Fig. 15.—*Amblyomma echidnae* (female). *a,* Scutum; *b,* capitulum (dorsal view); *c,* coxae I-IV; *d,* tarsi I and IV; *e,* spiracular plate. The straight lines each represent 0.5 mm.

Three Australian species have a hypostome dentition formula of 3/3, namely *A. postoculatum, A. helvolum,* and *A. sternae. A. sternae* may be readily distinguished from the other two species by its extensive ornamentation and punctation patterns.

AMBLYOMMA ECHIDNAE, sp. nov.

Fig. 15*a-e*

Holotype.—Female, Oonoonba (near Townsville), north Queensland. June 1943 (C. R. Mulhearn). Host, spiny ant-eater. In the Queensland Museum.

Paratype.—Female, same data as holotype. In the Animal Health Station, Yeerongpilly, Queensland.

Diagnosis

A large tick; scutum triangular, the scapulae pointed and deflected, extensively ornate; punctations unequal, not numerous, a short, deep depression in each lateral field; posterior margin of basis capituli concave, the postero-lateral angles swollen but barely salient; porose areas broadly oval and divergent; coxa I with 2 short, subequal spurs, other coxae each with one short spur; tarsus I with a single terminal spur, other tarsi bicalcarate.

Description

Body.—Fully engorged, length 21.2 mm., greatest width 12.7 mm.; an elongate oval tick, the dorsum with scattered, small, pale hairs and well-marked grooves.

Scutum.—Length 3.0 mm., width 3.2 mm., slightly broader than long, the posterior angle relatively narrow, the postero-lateral margins slightly concave; scapulae pointed and deflected; emargination deep; ornate with a brown marginal band, very narrow along the posterior angle, median field brown, a rectangular pale spot in the posterior angle, cervical spots large and fused with the broad cervical stripes, which are divergent, elongated, and almost interrupted medianly, frontal spot narrow, elongate, fused with the cervical stripe and narrowly separated from a large ocular spot by a narrow pale bridge extending from the pale patch in the scapular fields, limiting spot large and somewhat semicircular; punctations unequal, not numerous, a few moderately coarse punctations in the lateral and scapular fields, a short but broad and deep depression in each lateral field near the eye; cervical grooves, deep, short, convergent, extending posteriorly by conspicuous, broad, and deep depressions, which become divergent and shallow and reach only a short distance into the posterior half of the scutum.

Capitulum.—Length 1.90 mm.; basis 1.06 mm. wide, the posterior margin concave, the postero-lateral angles swollen, rounded but barely salient, lateral margins convex, porose areas relatively large, broadly oval, their longer axes directed anteriorly and slightly divergent, the interval equal to their diameter; palpi 1.2 mm. long, stout, article 2 not quite twice the length of article 3; hypostome dentition formula 4/4 of about 6 relatively small teeth.

Venter.—Dark, with very scattered, small, pale hairs; genital opening slightly anterior to coxa II; ventral grooves well defined.

Legs.—Moderately long, slender, brown with pale joints; coxa I with 2 subequal, short spurs, the external the longer, coxae II-IV each with a single short spur; tarsus I stout, a little humped, and with a small terminal spur, tarsi II-IV more slender and bicalcarate with well-developed spurs.

Spiracular plate.—Shape as in Figure 15*e*, 0.8 by 0.72 mm.

Comments

Both ticks have been poorly preserved in alcohol and the scutal colour pattern is indistinct. In the holotype there are traces of colour along the inner border of the cervical grooves, but these are too indistinct to mention in the description.

The colour pattern of the paratype appears to be more extensive than that of the holotype and the dark areas are less well defined. The frontal spot is larger, fused with the ocular spot, and separated from the cervical stripe by a narrow bridge. The cervical stripe is narrow and elongate. The posterior angle has an extensive, triangular pale patch, which extends forwards between the cervical depressions. The porose areas are more subcircular than oval.

ACKNOWLEDGMENTS

The writer wishes to acknowledge the assistance given by the authorities of the various Institutions listed on pp. 112-3 in supplying material for study. Thanks are also extended to R. K. Keith, Technical Officer, Division of Animal Health and Production, C.S.I.R.O., and R. A. J. Meyers, Technical Officer, Division of Entomology, C.S.I.R.O., for their assistance with the figures.

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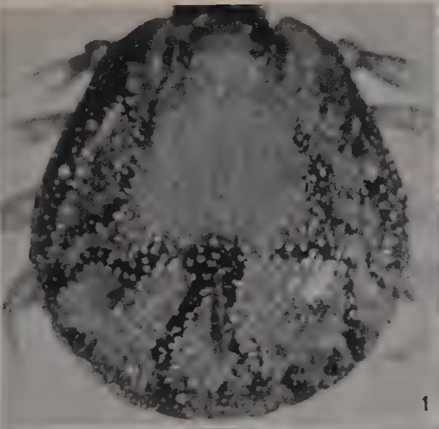
List of Species

Genus *Aponomma*	
A. auruginans Schultz 1936	123
A. decorosum (L. Koch 1867)	130
A. ecinctum Neumann 1901	136
A. hydrosauri (Denny 1843)	119
A. pulchrum, sp. nov.	140
A. quadratum Cooper & Robinson 1908	137
A. simplex Cooper & Robinson 1908	132
A. tachyglossi, sp. nov.	126
A. trachysauri (Lucas 1861)	115
A. trimaculatum (Lucas 1878)	138
A. tropicum, sp. nov.	128

Genus *Amblyomma*	
A. albolimbatum Neumann 1907	147
A. australiense Neumann 1905	146
A. echidnae, sp. nov.	158
A. helvolum Koch 1844	146
A. limbatum Neumann 1899	148
A. macropi, sp. nov.	153
A. moreliae (L. Koch 1867)	146
A. moyi, sp. nov.	151
A. papuana Hirst 1914	145
A. postoculatum Neumann 1899	145
A. sternae, sp. nov.	155
A. triguttatum Koch 1844	148



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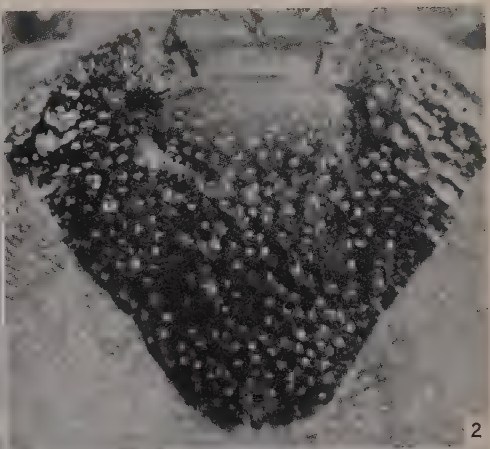

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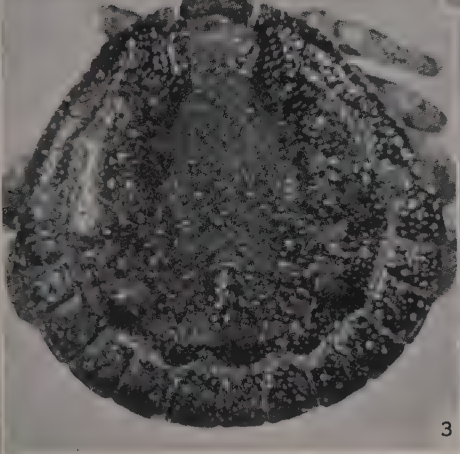

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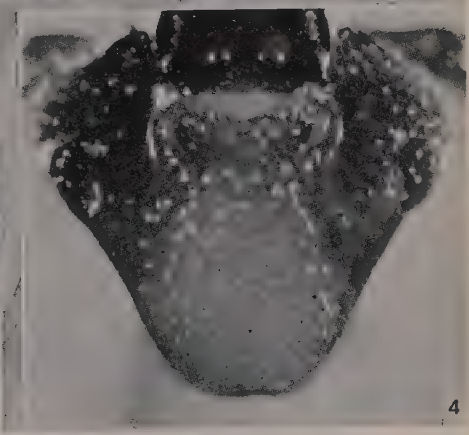

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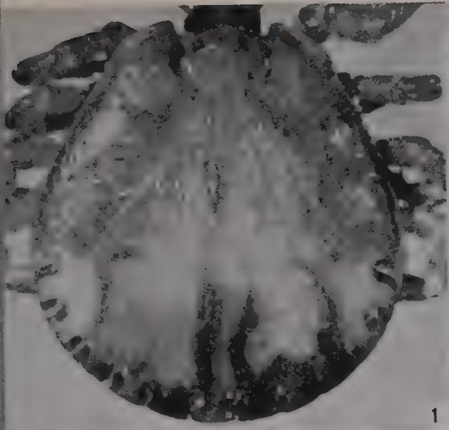
Fig. 1.—*Aponomma hydrosauri,* scutum of male. × 20.
Fig. 2.—*A. trachysauri,* scutum of female. × 30.
Fig. 3.—*A. trachysauri,* scutum of male. × 15.
Fig. 4.—*A. hydrosauri,* scutum of female. × 30.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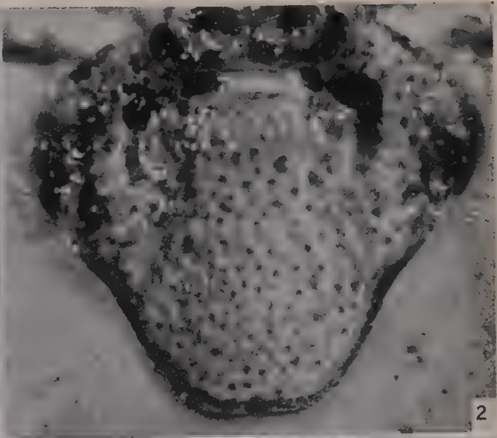
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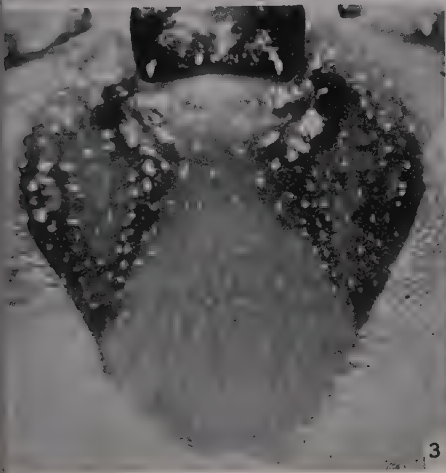
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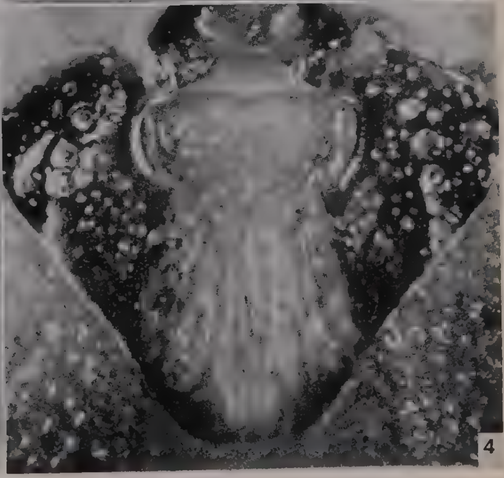
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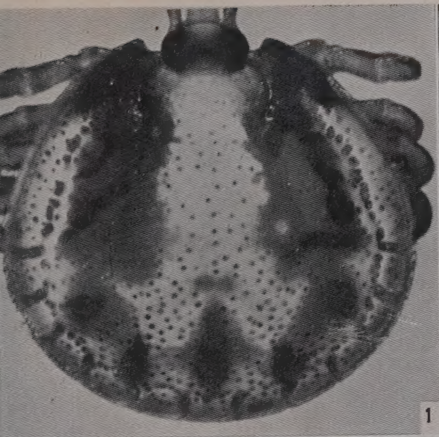
Fig. 1.—*Aponomma auruginans*, scutum of male. × 20.
Fig. 2.—*A. tropicum*, scutum of female. × 40.
Fig. 3.—*A. auruginans*, scutum of female. × 35.
Fig. 4.—*A. tachyglossi*, scutum of female. × 25.



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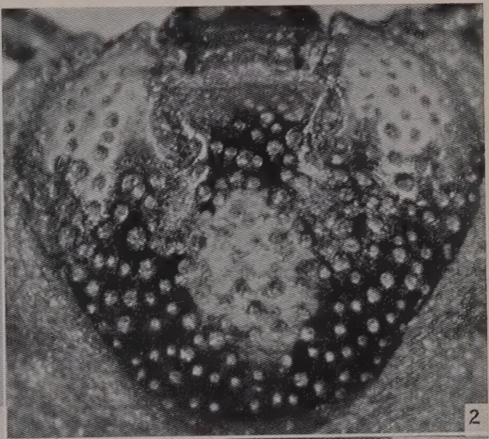

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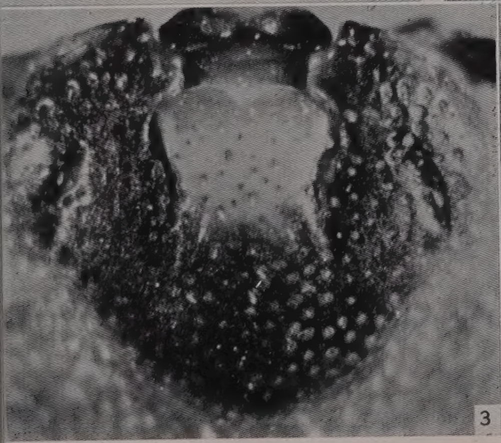

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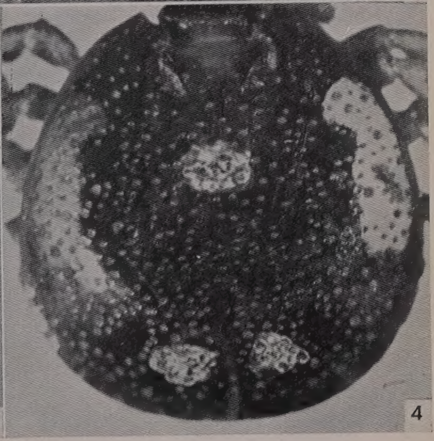

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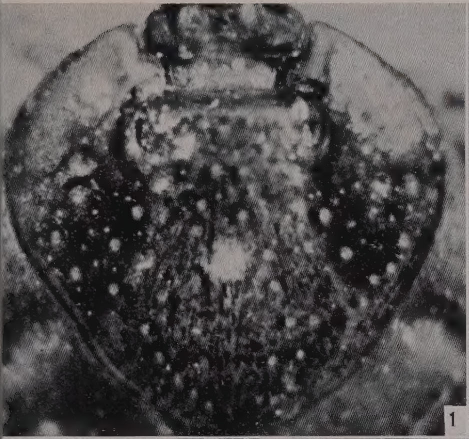
Fig. 1.—*Aponomma decorosum*, scutum of male. × 25.
Fig. 2.—*A. simplex*, scutum of female. × 40.
Fig. 3.—*A. decorosum*, scutum of female. × 40.
Fig. 4.—*A. simplex*, scutum of male. × 25.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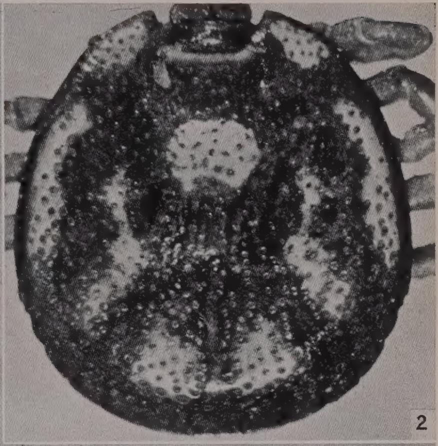
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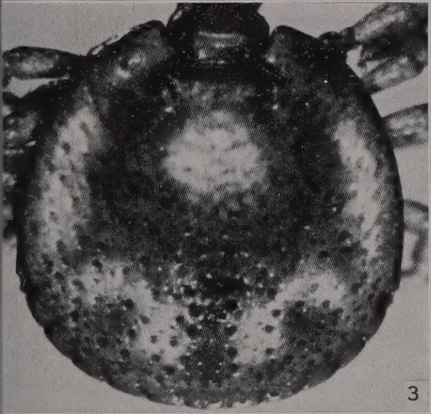
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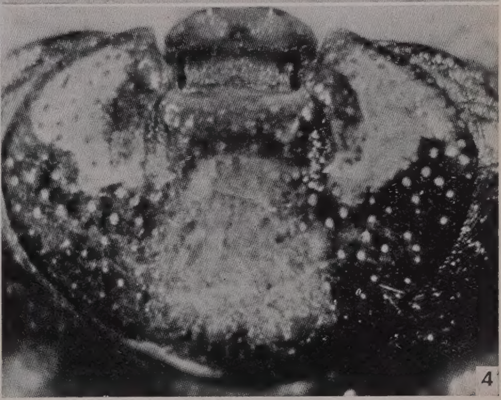
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Fig. 1.—*Aponomma trimaculatum*, scutum of female. × 40.
Fig. 2.—*A. pulchrum*, scutum of male. × 25.
Fig. 3.—*A. trimaculatum*, scutum of male. × 35.
Fig. 4.—*A. pulchrum*, scutum of female. × 35.